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THE BRITISH SILURIAN CYSTOIDS

BY

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THE BRITISH SILURIAN CYSTOIDS

By C. R. C. PAUL

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SYNOPSIS

The British Silurian cystoid fauna consists of the Echinoencrinitidae and Callocystitidae. It has a very restricted distribution conditioned by depth of water. It ranges from the Wenlock Shale possibly to the Aymestry Limestone. The Echinoencrinitidae originated from the Baltic, the Callocystitidae from N. America.

All the species were permanently fixed except *Schizocystis armata* (Forbes) which was vagrant. The 2- and 3-rhombed forms of *S. armata* had slightly different modes of life. Two trends in feeding, which are widespread among stemmed pelmatozoa, are recognized in the fixed forms. The rhombs were probably respiratory, the two half-rhombs being modified as inlet and outlet. The current pattern derived is widespread among cystoids.

The Glyptocystitida had 7 oral plates not 5, and *Pseudocrinites* has two brachioles representing ambulacra 1 and 4.

The growth of the stem, theca and subvective system is briefly described. Colour bands in the thecal plates may indicate that all species lived less than five years.

The fauna is described. *Tetracystis* and *Prunocystites fletcheri* Forbes are transferred to the Staurocystinae on their ambulacral structure. *Glansicystis* gen. nov. is described for " *Prunocystites* " *baccatus* (Forbes). *Pseudocrinites pyriformis* sp. nov. is described.

I. INTRODUCTION

The British Silurian cystoids form a distinctive and separate element of the British cystoid fauna and it is convenient to deal with them separately. The fauna contains all the British representatives of the families Echinoencrinitidae and Callocystitidae. All but one of the species present have been known since 1848 when Edward Forbes described all the then known British cystoids. This fauna is a particularly important one from the point of view of taxonomy. No less than six of the seven genera present are represented by their type species! It is also important from the point of view of palaeoecology and provides a unique glimpse at the mode of life of these extinct pelmatozoans. Little has been added since 1848 to the descriptions given by Forbes although the number of specimens found has increased considerably. Certain inaccuracies in the original descriptions have survived to the present as a result. The fauna consists of the following :

Family **CALLOCYSTITIDAE** Bernard

Subfamily **STAUROCYSTINAE** Jaekel

Staurocystis quadrifasciatus (Pearce)
Pseudocrinites bifasciatus Pearce
Pseudocrinites pyriformis sp. nov.
Tetracystis oblongus (Forbes)
Prunocystites fletcheri Forbes

Subfamily **APIOCYSTITINAE** Jaekel

Apiocystites pentrematoides Forbes

Family **ECHINOENCRINITIDAE** Bather

Subfamily **SCOLIOCYSTINAE** Jaekel emend.

Glansicystis baccata (Forbes)
Schizocystis armata (Forbes)

II. ACKNOWLEDGMENTS

The writer gratefully acknowledges the help of Dr. R. P. S. Jefferies and Mr. H. G. Owen of the British Museum, Natural History (BMNH.), Mr. R. G. Coope of the Department of Geology, Birmingham University (BU.), Mr. C. D. Waterston of the Royal Scottish Museum (RSM.), Mr. H. P. Powell of the Department of Geology, Oxford University Museum (OUM.), Mr. A. Wilson of Dudley Central Library (DL.), Mr. A. G. Brighton of the Sedgwick Museum (SM.), and Mr. R. V. Melville of the

Geological Survey & Museum (GSM.), for the loan of material or access to specimens in their care. The author is also indebted to Dr. Mutvei of the Naturhistoriska Riksmuseum, Stockholm (RM.), for the loan of comparative material of *Lovenicystis angelini* and *Echinoencrinites* and to Dr. P. M. Kier of the U.S. National Museum for the loan of specimens of *Pseudocrinites perdewi*. Mr. M. L. K. Curtis of Bristol Museum supplied the information concerning Pearce's types and Dr. I. Strachan and Mr. R. G. Coope of Birmingham University information on the detailed stratigraphy of the Wenlock Limestone at Dudley. Mr. A. Barlow assisted in the preparation of the text-figures.

Very useful discussion on the functioning of the rhombs and the mode of life of *Pseudocrinites* was contributed by Dr. R. P. S. Jefferies and by Mr. P. Minton of Imperial College but the writer alone accepts responsibility for the views expressed in the paper.

This research was completed during the tenure of a Science Research Council research studentship under the direction of Mr. A. G. Brighton, and partly, during the tenure of a Harkness Scholarship, both of which are gratefully acknowledged. Finally the writer wishes to thank Professor O. M. B. Bulman for research facilities in the Sedgwick Museum, Cambridge.

III. GEOGRAPHICAL DISTRIBUTION AND STRATIGRAPHIC RANGE

None of the species dealt with in the present work is known from outside the British Isles and all have a very restricted distribution. Text-fig. 1 shows that this restriction is quite independent of the outcrop distribution and was almost certainly controlled by contemporaneous environmental factors. *Schizocystis armata* (Forbes) occurs in the Wenlock Shale and is found at all the localities shown on Text-fig. 1. The remarkable similarity in distribution shown by *Schizocystis*, in the Lower Wenlock, and the shallow water brachiopod communities established by Ziegler (1965), in the preceding Upper Llandovery, is unlikely to be due to coincidence and it is suggested that the distribution of *Schizocystis* was controlled by depth. All the other species, except *Pseudocrinites pyriformis* sp. nov., are confined to the Wenlock Limestone of Dudley (Wren's Nest and Castle Hill) and possibly the Walsall Inlier also in the cases of *Staurocystis quadrifasciatus*, *Pseudocrinites bifasciatus* and *Glansicystis baccata*. These localities are on the extreme easterly margin of the outcrop of the Wenlock Limestone and may indicate that these species lived in even shallower water. *Pseudocrinites pyriformis* is believed to come from the Sedgley (Aymestry) Limestone of the Sedgley Inlier which is again near the easterly margin of the outcrop and indicates a similar environment for that species too.

Text-fig. 2 shows the succession of cystoid bearing strata at Dudley. *Schizocystis armata* is recorded from Hurst Hill, in the Sedgley Inlier, and Dudley, where only the top 100–150 ft. of the Wenlock Shale outcrop. However, beyond this, little can be said about its distribution within the Wenlock Shale and it may well range throughout the formation. Many museum specimens of the Wenlock Limestone species are preserved on slabs of crystalline limestone composed largely of echinoderm

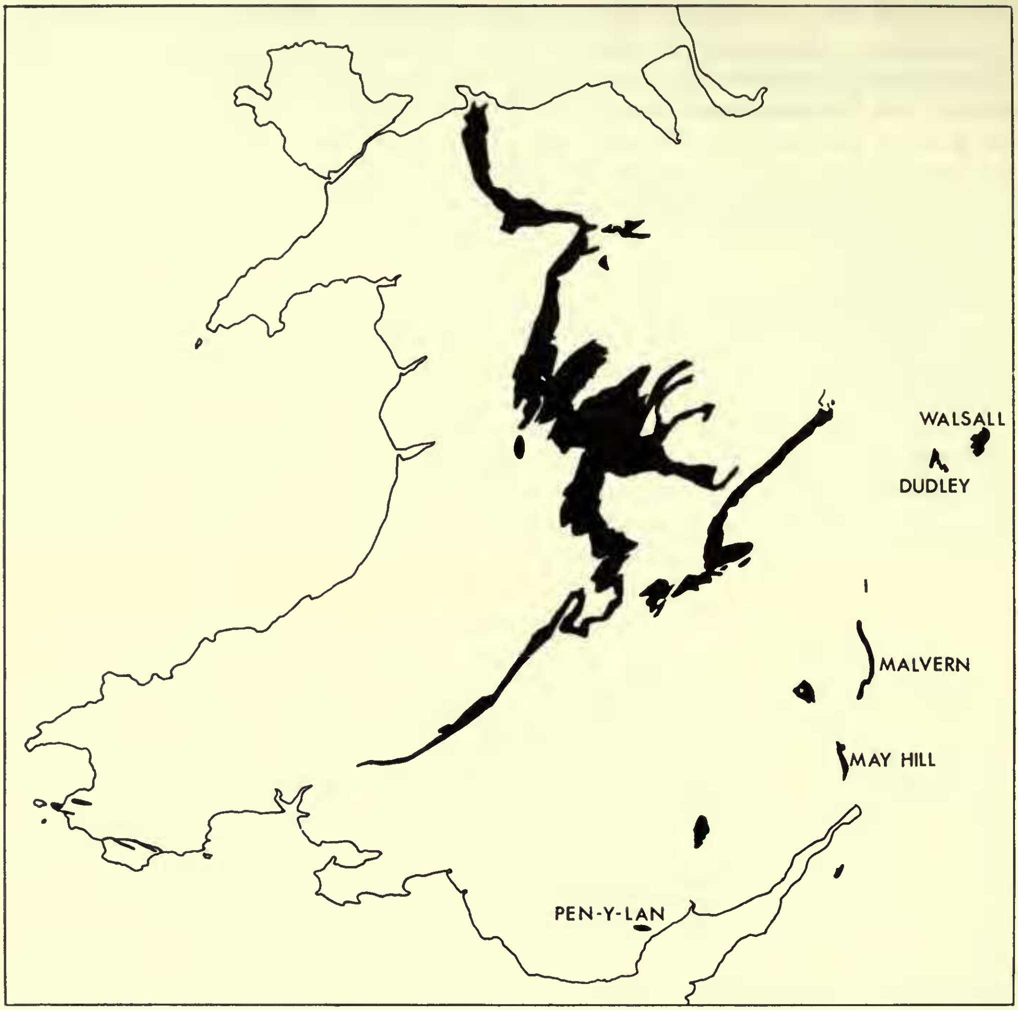


FIG. 1. Map showing the outcrop of rocks of Wenlock and Ludlow age and the cystoid localities. Dudley is used in a broad sense including the Wren's Nest, Castle Hill and the Sedgley Inlier. Compare with the depth zones established in the Llandovery by Ziegler 1965.

debris and with a thin veneer of shale on the surface on which the cystoids are preserved. A large number of crinoids are also found in this type of preservation and both the cystoids and the crinoids are usually well preserved with stems, brachioles and pinnules intact and attached to the thecae or calyces. There is some evidence to suggest that all these specimens originate from the same horizon, namely a shale parting about half way up the Lower Limestone. Almost certainly this horizon represents a catastrophe in which the contemporary echinoderm fauna was exterminated by a sudden influx of mud. There are many other specimens preserved in different lithologies whose exact provenance is unknown however.

The only two specimens of *Pseudocrinites pyriformis* known are in the Holcroft collection in the Department of Geology, Birmingham University. Holcroft was one of the few people who recorded exact localities and these specimens are said to have come from Sedgley. Other specimens in the same collection are recorded as

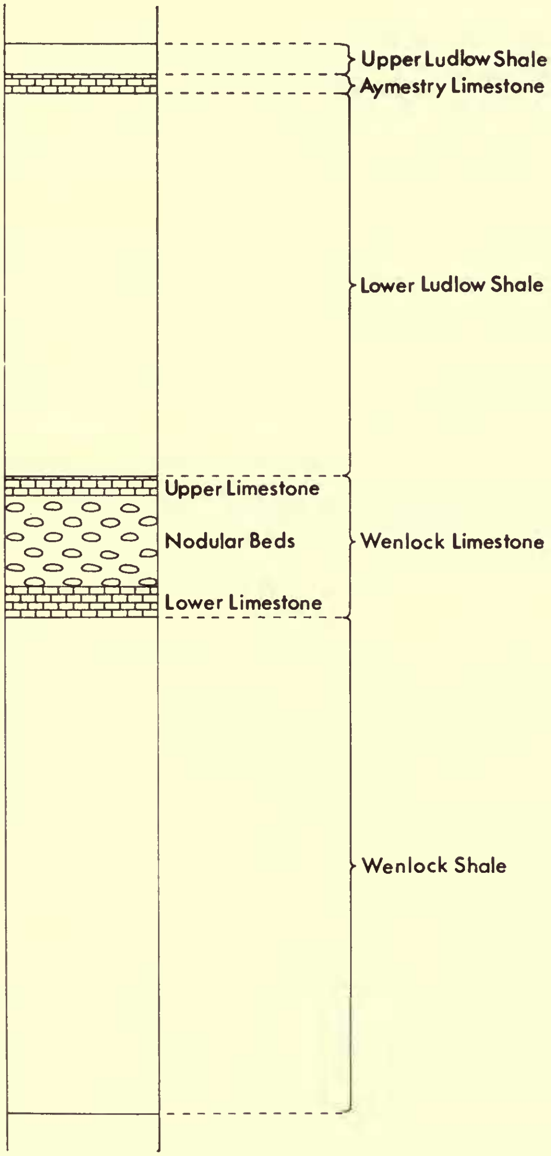


FIG. 2. Stratigraphic succession of Silurian cystoid bearing rocks at Dudley.

coming from Hurst Hill, also in the Sedgley Inlier. All the Wenlock rocks in the Sedgley Inlier are confined to the immediate vicinity of Hurst Hill while the vast majority of the Sedgley Inlier, including that part on which Sedgley itself is built, is of Ludlow rocks and both Mr. Coope and Dr. Strachan, of the Geology Department, Birmingham University, inform me that it is likely that these specimens came from the Sedgley Limestone at Sedgley. In this case they are considerably younger than all the other species described here.

IV. RELATIONSHIPS TO OTHER FAUNAS

Schizocystis and *Glansicystis* are endemic to Britain and the last representatives of the Echinoecrinitidae. All other echinoencrinitids are confined to the Ordovician of the Baltic States and Scandinavia. This element of the fauna had a Baltic origin therefore and represents an evolutionary dead end.

Lovenicystis angelini (Jaekel) from Gotland, Sweden, is the only member of the Callocystitidae, apart from the British forms, to occur outside North America. The family ranges from the Upper Ordovician to the Middle Devonian and the British fauna probably represents an evolutionary sideline which migrated across to Europe. It is possible that the Staurocystinae evolved in the British Isles and later migrated back to North America. This subfamily apparently attains its maximum diversity in Britain and appears earlier here than in the United States.

V. FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

In dealing with the morphology of the cystoids it is convenient to consider the stem, the theca, and the subvective system separately.

a. *The Stem*

All the species described had a well developed stem and all except *Schizocystis* probably had a root structure, but it has not been possible to confirm this in *Tetracystis oblongus* or *Prunocystites fletcheri*. The stem is characteristic of the superfamily Glyptocystitida, to which all the present species belong, and is divisible into proximal and distal portions. The proximal portion of the stem is composed of thin, ring-like columnals with a wide lumen, and usually tapers rapidly away from the base of the theca. There are two sorts of proximals : large outer proximals and smaller inner proximals. The outer proximals fit outside the inner proximals and are provided with an internal flange against which the two adjacent inner columnals fit. Externally they may have a flange or a ring of spines or tubercles. Alternating with the outer proximals throughout the proximal portion of the stem are the inner proximals. These are thin rings which are frequently hidden from view by the outer proximals. The internal flange of the outer proximals is provided with two swellings set opposite each other which are interpreted as fulcra. Similarly the upper and lower surfaces of the inner proximals are provided with slight swellings which were probably facets. In *Cheirocrinus* it is known that the fulcra on the upper and lower surfaces of the outer proximals are set at slightly different positions so that the axis of rotation was different for successive pairs of proximals. It has been impossible to confirm that the same arrangement obtained in the British Silurian cystoids but it is certain that the proximal stem was very flexible. Several have been preserved quite tightly curved but still articulated.

The distal portion of the stem was also composed of two sorts of columnals but arranged one above the other. This alternation is not always obvious but was almost certainly present. The distals of both types were relatively tall and narrow in diameter with a narrow lumen. The distal stem generally tapers much less rapidly and in forms with a root structure may not taper at all. The larger distals are the morphological homologues of the outer proximals and are flanged in the species with flanged outer proximals. The smaller distals are, correspondingly, the homologues of the inner proximals. At the termination of the distal stem there is frequently a swelling or some irregular branches which form a root structure. All species with a root structure are believed to have been attached permanently and therefore relied on food-bearing currents coming to them. A flexible stem would be of advantage in that it would allow them to sweep a considerable area around the point of attachment. In forms like *Glansicystis* it would allow the apex of the theca to be directed upwards at all times. It would also allow flexure in currents and thus reduce the chances of the stem snapping. Finally it would raise the theca up off the substrate thus allowing the food collecting apparatus to collect falling food particles before they reached bottom dwelling forms and keep the rhombs and food collecting apparatus well clear of the turbulent zone just above the bottom, reducing the chances of fouling by mud particles. All species without a root structure are believed to have been free and vagrant. Among the present species this includes only *Schizocystis armata* which is believed to have used the stem as an organ of locomotion. *Schizocystis* is a special case and will be dealt with in a separate section.

b. *The Theca*

In *Pseudocrinites* the theca is more or less distinctly lenticular but in all the other species it is ovoid. The mouth was apical and the anus lateral and set fairly high up on the theca. The latter opened in a periproct covered by an anal pyramid surrounded by a single circlet of auxiliary plates. This circlet may be complete or incomplete, apparently even in the same species, and it is difficult to see what function it could have served. It may simply be the remnant of the extensive plated periproctal membrane of the ancestral group, the Cheirocrinidae. The anal pyramid forms a one-way valve system closed either by ligamental or muscular action. There is no indication of any musculature to open the valve and this must be assumed to have been achieved by peristaltic action. As a result the faeces would have been pellet-like and very unlikely to have fouled either respiratory or food bearing currents. Despite its high position on the theca the anus is placed well away from the pectinirhombs which are at the same level as the anus and the single rhomb below it is on the opposite side of the theca. In the Callocystitidae, where the arms are folded down the theca, the food grooves of the brachioles are directed towards the centre of the arms and therefore away from the anus in the ambulacra adjacent to it. There are two orifices higher up on the theca usually accepted as the hydropore and gonopore. One is circular and frequently covered by a pyramid of plates resembling a small anal pyramid. This orifice almost certainly acted as an exit and is therefore accepted as the gonopore. Adoral to it, and curved round it in many cases, is a slit-like orifice provided with a rim and usually swelling out at either end. This is accepted as the hydropore. These two orifices are always above rhomb L1 : R5 and are taken as the fundamental point for orientating the theca. The ambulacrum which passes between the anus and the hydropore and gonopore in the Glyptocystitida is always ambulacrum 5.

The theca of the glyptocystitid cystoids is composed of a definite number of thecal plates arranged in definite circlets. The formula 4 basals (BB), 5 infralaterals (ILL), 5 laterals (LL), 5 radials (RR), and 5 orals (OO) is usually given. The ancestral genus, *Cheirocrinus*, had 6 radials and occasionally examples of other species occur with extra plates but on the whole the formula applies for the first four circlets. In the case of the orals however, it is possible that the usual pentamery of echinoderms has caused the acceptance of too low a number. There were apparently 7 orals in the Glyptocystitida. Kesling (1961*a*, 1961*b*, 1962*a*, 1962*b*) and Kesling & Mintz (1961) have figured the oral areas of *Glyptocystites ehlersi* Kesling, *Jaekelocystis hartleyi* Schuchert, *Rhombifera bohemica* Barrande, *Cheirocrinus anatiformis* (Hall) and *Lepadocystis moorei* (Meek). In all cases there were 7 plates in the oral area and O1 was interpreted as being compound. To these species can be added *Glansicystis baccata* (Forbes), *Schizocystis armata* (Forbes), *Apiocystites pentrematoides* Forbes, *Staurocystis quadrifasciatus* (Pearce) and *Pseudocrinites bifasciatus* Pearce, all with 7 orals. *Pleurocystites* probably had 7 orals too. If all these interpretations are correct 7 orals are known in six of the seven families within the Glyptocystitida and this situation would seem to be of general occurrence. Text-fig. 3 shows the interpretation adopted here. OO2–5 are the same as in all previous interpretations. O1 is the plate bearing the left portions of the gonopore and hydropore as viewed facing these pores. O7 bears the other portions of these orifices and the small plate, adoral to O7, is O6. This interpretation commends itself as in

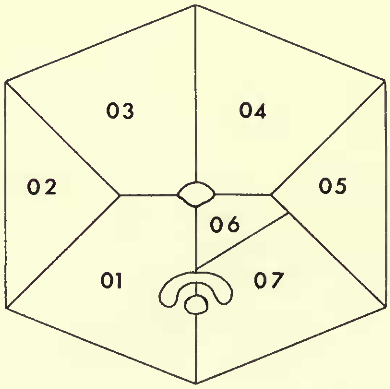


FIG. 3. Schematic representation of the arrangement of oral plates in the Glyptocystitida. OO, orals.

some cases the common suture of O7 and O6 runs from O1 to R5 and in this case the 7 orals form a ring with the plates numbered consecutively.

When fully developed all the rhombs are disjunct pectinirhombs. This type of disjunct pectinirhomb is formed of pore-canals, called dichopores, which are basically folds in the surface of the theca. The walls of adjacent dichopores are confluent and all the dichopores open collectively in *vestibules*. As with all rhombs they are shared between two thecal plates and the common plate suture divides the rhomb into two *half-rhombs*. The width of a rhomb is measured along the plate suture. At right angles to the suture lies the *rhomb axis* which divides the rhomb into two *demi-rhombs* and along which the length of the rhomb is measured. Rhombs in which the length exceeds the width are called *compressed* and the converse *depressed*. When the two half-rhombs are unequal the rhomb is *unequal* and when the two demi-rhombs are unequal it is *asymmetrical*.

Rhombs are developed in three positions in all the species dealt with. These are across the sutures between plates B2 : IL2, L1 : R5 and L4 : R3. As far as is known B2 : IL2 is not developed in *Prunocystites fletcheri* and *Schizocystis armata* sometimes lacks L1 : R5. Otherwise all three rhombs are developed in all species. When fully developed there is a constant difference between the two half-rhombs of each rhomb. The half-rhombs B2, R5, and R3 all have a raised rim on the absutural side of the series of slits and the slits are generally longer than the corresponding slits of the other half-rhombs. In half-rhombs IL2, L1, and L4 there is a continuous raised rim running around the slits on both the ad- and absutural sides. In several cases the slits are very slightly wider in these half-rhombs than in the preceding half-rhombs.

Two trends can be seen in the shape of the rhombs and these can, to a certain extent, be related to the maximum size of the thecae in which they occur. In *Pseudocrinites*, and other genera or species with relatively large thecae, the rhombs tend to be large, depressed and asymmetrical. They are angular in outline and provided with a large number of dichopores. In forms like *Glansicystis*, with relatively small thecae, the rhombs tend to be distinctly compressed, symmetrical and the half-rhombs tend to be semi-circular in outline. The number of dichopores rarely exceeds 10. *Schizocystis*, which has this type of rhomb and a relatively large theca, has an unusually large number of dichopores in its rhombs (up to about 20) but still less than in the rhombs of *Pseudocrinites*.

The constant difference between the two half-rhombs is interpreted as being associated with the functioning of the rhombs. Sinclair (1948) postulated that there were ciliary currents flowing through the dichopores in life. In the rhombs of *Glyptocystites*, which have no absutural rims but an adsutural rim on one half-rhomb, he suggested the rim assisted in preventing re-circulation of the currents. The half-rhomb with the rim was therefore the exit and the other the entrance. All further investigations made by the present writer tend to confirm this interpretation. The closed rim of the rhombs in the present species is interpreted as a mechanical barrier to re-circulation. In *Staurocystis* it is known that the slits of one specimen (BU. Hol, rhomb L1 : R5) are narrower in the incurrent half-rhomb than in the excurrent. This may be a device to prevent harmful particles or organisms entering and clogging the dichopores. The extra length of the incurrent slits may be the result of an attempt to achieve the same cross-sectional area while decreasing the width. Alternatively in some cases the slits of the two half-rhombs appear to be of the same width and in these cases the excurrent would have been stronger than the incurrent. This is known in other cystoids with different types of rhombs and also in blastoids. Thus Macurda (1966) has been able to show that the excurrent from the hydrospires of *Globoblastus norwoodi* was six times as fast as the incurrent. In this case, and in others the present writer has investigated, there can be no doubt as to which way the currents were flowing. Such an arrangement may be of advantage in directing a strong current away from the theca and thus reducing the chances of recirculation by surface ciliary currents.

The trends in the outline of the rhombs are probably a result of the maximum size of the thecae in which they occur. Assuming the rhombs were respiratory, larger thecae would require more oxygen and therefore larger rhombs. This could be achieved by either lengthening the dichopores or increasing their number. The latter is likely to be more efficient since there must be a length in which all the available oxygen will be removed. Increasing the length beyond this will not increase the efficiency of the rhombs. It is significant that in one of the largest rhombs examined by the writer (L1 : R5 in *Pseudocrinites gordoni*, BMNH. E. 23122) the longest dichopore was 6·45 mm. and there were approximately 85 dichopores in 14·85 mm. However, in rhomb L4 : R3 of *Echinoencrinites* cf. *reticulatus* (RM. Ec.5515) the longest dichopore is 6·7 mm. but there are only 9 dichopores in a width of 3·7 mm. Apparently the longest dichopores of both types of rhomb are about the same length. It must be pointed out, however, that the size and shape of a rhomb is controlled by the plates in which it is developed. Thus a rhomb developed across a short suture has a much smaller potential width than one developed across a long one. This in turn is to a certain extent, controlled by the size and shape of the thecae as a whole.

Considering the theca as a whole it is possible to deduce a current pattern for the three rhombs. If the above interpretations are correct then water entered the rhombs at the ab- and adoral extremities of the theca and passed out near the ambitus. In all forms of cystoids in which the current patterns have been determined they are the same, i.e. in at the extremities and out near the ambitus. In *Glyptocystites* and *Cheirocrinus* there were some additional currents running around the theca and *Cystoblastus* and *Rhombifera* represent a departure to a condition where all the currents ran around the theca. Unfortunately sufficiently well preserved specimens of these genera are not available and the current patterns remain unknown in detail.

c. *The Subvective System*

By analogy with living crinoids this system functioned as the food collecting apparatus of the cystoids. The fixed species may be conveniently divided into two groups on the basis of their ambulacral structure. These are: species with the ambulacra folded down the sides of the theca, and those with the ambulacra restricted to the apical region of the test. In the former there are usually four ambulacra but *Pseudocrinites* represents a special case and only has two ambulacra. By analogy with species of callocystitids with the full five ambulacra, the four present in most British species are accepted as 1, 2, 4 and 5, the last being the ambulacrum passing between the anus and the gonopore. For descriptive purposes it is convenient to number the brachioles in each ambulacrum in the order in which they developed.

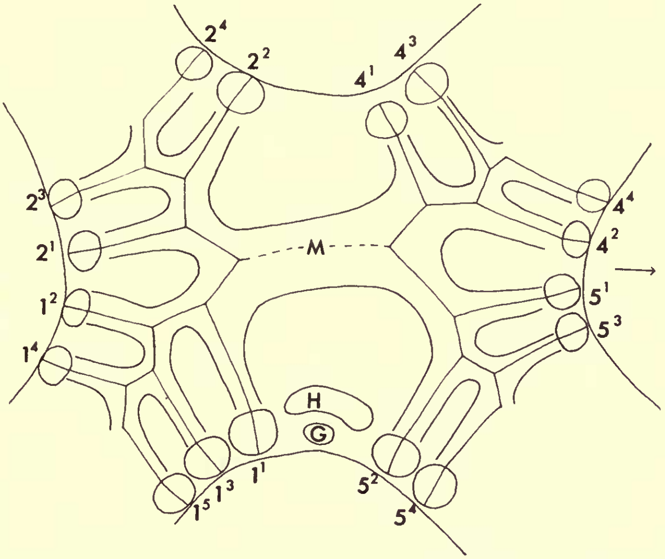


FIG. 4. *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of apical region to show arrangement of the ambulacra and brachiole numbering system. G, gonopore; H, hydropore; M, approximate position of mouth. The arrow points to the periproct. The ambulacrum passing between the anus and gonopore is ambulacrum 5. BMNH. 48197.

Thus the first formed brachiole of ambulacrum 2 is 2^1 (see Text-fig. 4). In all the British species the first formed brachiole of each ambulacrum is branched off to the left, looking down the ambulacrum from the mouth to the tip. The second formed brachiole is on the right in all species with four ambulacra and the brachioles alternate regularly throughout the length of the ambulacrum. In both species of *Pseudocrinites* described here there are two facets on the left adapically in each ambulacrum. It is suggested that the two adoral facets are all that remains of the two ambulacra missing in this genus (see Text-figs. 16, 21). Kesling (1961*b*) has shown that the two fully developed ambulacra in *Pseudocrinites* are 2 and 5 and so it is suggested here that the three adoral brachioles in ambulacrum 2 are 1^1, 2^1 and 2^2, while those in ambulacrum 5 are 4^1, 5^1 and 5^2.

The ambulacra in the first group are composed of two series of alternating large and small flooring plates (see Text-fig. 10). The larger alternate about the median line and the smaller are inserted between them at the outside edge. One each of both types contributed to the formation of a brachiole facet with the smaller forming the adoral portion in all cases. Along the zigzag suture between the two rows of primary flooring plates ran the main food groove. At each change of direction it gave off lateral branches running to the brachioles. These were biserial structures with a food groove running down the side facing the main food groove. Both the " arms " and the brachioles were provided with cover plates over their food grooves. It is possible that the cover plates of the " arms " were immobile and therefore that food collection was confined to the brachioles. There were apparently three cover plates to every brachiolar in the brachioles. The structure of the brachioles indicates that they were incapable of twisting about their axes and therefore it would be advantageous to have the food grooves facing any food bearing currents. From the disposition of the ambulacra food collecting would seem to have been confined to four, or in *Pseudocrinites* two, *zones of collection.* The brachioles were capable of curling inwards over the ambulacrum. It is not certain whether this was a protective action or simply the position adopted when at rest. When feeding the brachioles would have been extended and this was probably achieved by hydrostatic action. If so the orientation of the facets gives an indication of the width and cross-section of the zones of collection.

Pseudocrinites would seem to have been at a disadvantage compared with the other species. Not only did it have half the potential number of brachioles of its nearest relative, *Staurocystis quadrifasciatus*, but the brachioles were set further apart. There were also only two dozen brachiolars in each brachiole in *P. bifasciatus* as opposed to three dozen in *Staurocystis.* From the lenticular shape of the theca of *P. bifasciatus* one may infer that if it turned edge-on to any currents it would have brought one zone of collection to face the current and reduced resistance to the current. If the current periodically reversed both zones could function with very little twisting of the stem. The most obvious reversing current is a tidal one. *Pseudocrinites pyriformis* presumably had a similar mode of life although it had longer brachioles and ambulacra which did not extend as far down the sides of the theca.

In *Glansicystis*, and possibly also *Prunocystites*, the brachioles are grouped about the mouth and the food grooves on the theca are very short. The brachioles have their food grooves on the adoral side and thus form an apical *cone of collection.* This arrangement is much better adapted to collecting falling food particles. From the position of the food collecting apparatus it may be inferred that the British Callocystitidae were better adapted to take advantage of currents in a relatively agitated sea while *Glansicystis* was better able to take advantage of falling food particles in a relatively still sea. These appear to be two extreme conditions which are found randomly distributed among stemmed Pelmatozoa.

d. *Schizocystis armata* (Forbes)

As mentioned previously this species differs in most respects from all the others dealt with. It is found over a much wider, though still restricted, area. It is apparently confined to the Wenlock Shale and thus lived in a muddy environment. In its morphology it has one very important difference in lacking a root structure.

Kirk (1911) has shown that many stemmed pelmatozoa were in fact vagrant. It is unfortunate that he chose as some of his examples British Silurian species which are now known to have been attached permanently but his main contention is not invalidated by this. It is not unreasonable to assume that all stemmed pelmatozoans which lack a definite root structure were voluntarily vagrant, at least temporarily, during their life-time. If food supplies were erratic temporary fixation would only be of advantage if the animal could voluntarily free itself. One must infer that forms like *Ancyrocrinus* literally weighed anchor and sought new feeding grounds in times of short supply. Such activity is known in Recent free living crinoids (which in general lack a stem) and may be inferred for extinct ones. On the above reasoning *Schizocystis* was probably vagrant, and used its stem as a tail.

The theca, like the stem, is on the same basic plan as the other species but has differences in detail. It is very variable in form and ornamentation but is generally compressed adorally and this may be an attempt to develop a bilateral symmetry. Taking the anus as posterior the compression is lateral and the two flattened areas correspond to the left and right sides. In many examples the right side is gently convex throughout but the left side is concave or flat adorally and convex aborally. The rhomb L1 : R5, which is often undeveloped, lies on the left side of the theca.

There are two ambulacra, running posteriorly and anteriorly along the crest of the theca. The posterior ambulacrum is the shorter and sometimes reaches the periproct. A curious feature of the ambulacra is that brachioles are developed predominantly on one side only. Brachioles are mainly developed on the left sides of both ambulacra and as a result the food grooves face the left side of the theca in the posterior ambulacrum and the right side in the anterior ambulacrum.

It is reasonable to assume that this species was benthonic, and since it lacks a root structure, that the theca lay on the substrate. Placing a theca on a flat surface the most stable position for it is lying on the left side. In the two-rhombed forms this leaves both rhombs clear of the substrate and the mud is unlikely to have fouled the rhombs. This is also true of the gonopore and hydropore which are developed on the left side in a raised portion of the test which is vertical in this orientation. The brachioles of the posterior ambulacrum could browse off the mud while those of the anterior ambulacrum would have their food grooves facing upwards and could possibly have fed off falling food particles. When the third rhomb is present it would have been useless in this orientation as it would have been fouled by the mud as would the gonopore and hydropore. The weight of the stem may have been used as a counterbalance to the theca and so the adoral part may have been kept off the substrate. There are difficulties in this suggestion. If the substrate was muddy the theca would have sunk in to some extent and the zone immediately above the surface would have been muddy if there was even slight turbulence. Possibly three-rhombed forms could tolerate having one inefficient rhomb since the two-rhombed forms tolerated the complete loss of one. It is difficult to explain the orientation of the food collecting apparatus and either this species was relatively poorly adapted to its new mode of life or it was trying to get the best of both worlds, feeding in the usual manner for the Echinoencrinitidae and browsing off the mud as well.

VI. GROWTH

a. *The Stem*

Plotting the graph (Text-fig. 5) of thecal height against the number of proximal columnals in *Staurocystis quadrifasciatus* indicates that there is considerable variation. A slightly better grouping is obtained by plotting the diameter of the top-most columnal against the total number of proximals (Text-fig. 6). Growth of the proximal stem was almost entirely confined to the addition of new columnals and this most likely took place at the base of the theca, as in living crinoids. In the distal stem growth was partly achieved by the addition of new distals and partly by the lengthening of existing distals. Since the large and small distals alternate regularly, in many cases, addition of new distals could not have been by the intercalation of " internodals " as in some crinoids. It is very unlikely that proximals migrated relatively down the stem and turned into distals after reaching a given point. This would require considerable changes in shape and the inner proximals would have to emerge from within the outer proximals. Almost certainly new distals were added at the junction of the distal and proximal portions of the stem and in some cases the topmost distals are thinner than succeeding ones and appear to be relatively newly formed.

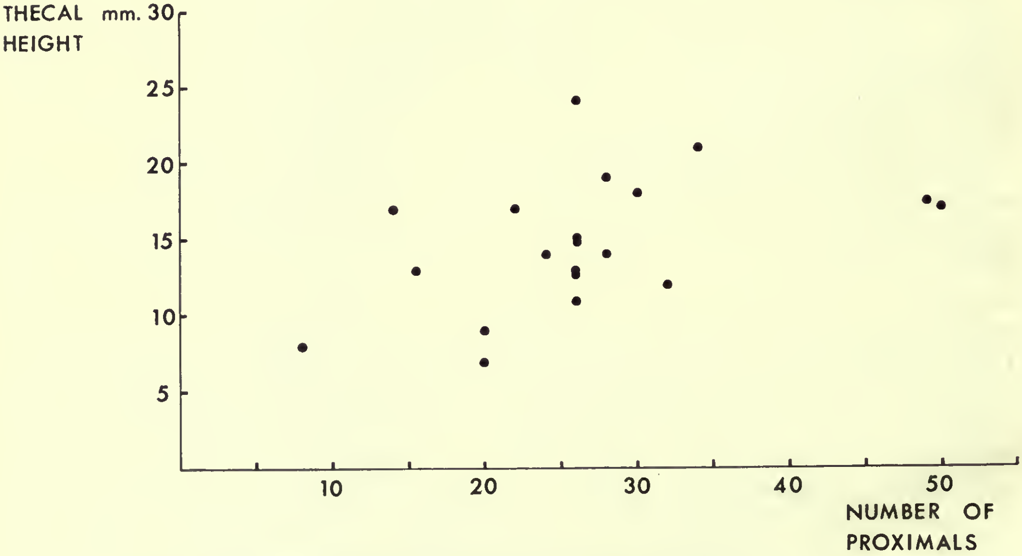


FIG. 5. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between thecal height and number of proximal columnals.

b. *The Theca*

All thecae known have the same number of thecal plates and within the size range examined growth was achieved by increasing the size of these plates and not by the addition of new plates. The smallest thecae known are still quite large, about 5 mm. in thecal diameter, so the earliest growth stages remain unknown. Fine growth lines are not very often preserved in these cystoids but growth can be shown to have been holoperipheral in all thecal plates. Some specimens of all species show colour banding on the plates which is associated with growth. This is most clearly shown in SM. A11160, a worn specimen of *Tetracystis oblonga* showing, on all plates visible, concentric light and dark bands. These bands are thickest where growth has been greatest and thinnest where growth has been least. B3 shows a central light coloured area followed outwards by four alternating dark and light bands and the suggestion of another dark band at the suture. These bands can be matched in other plates but in general the central light area is smaller relatively, particularly on the only radial plate clearly visible (R5). Measuring outwards from the centre of B3 towards the common suture with IL3, the thicknesses of the bands are as follows : 0·6 mm. 0·23 mm. 0·53 mm. 0·33 mm. and 0·27 mm., the vague suggestions of the outermost dark band are too indefinite to measure. The darker bands are generally thinner as is the case above (see Pl. 10, figs. 6, 13). Apparently the growth was periodic and the periods when darker calcite was deposited were either shorter or less favourable to calcite secretion. This was almost certainly a seasonal effect in which case the animal commenced growing in season favourable to calcite secretion and survived two lean periods, possibly up to the onset of a third. If these periods were annual, which is the most obvious suggestion, then the dark bands probably represent winter and this cystoid reached its present size in three years. No example seen exceeds five years. There is apparently no information on longevity and growth rates in living crinoids but in echinoids corollary growth rates can be found. The information available in four species gives coronal diameters of 24–90 mm. in three years (Hyman 1955 : 588), whereas the cystoid is 14 by *c.* 8 by *c.* 11 mm. The mode of growth of

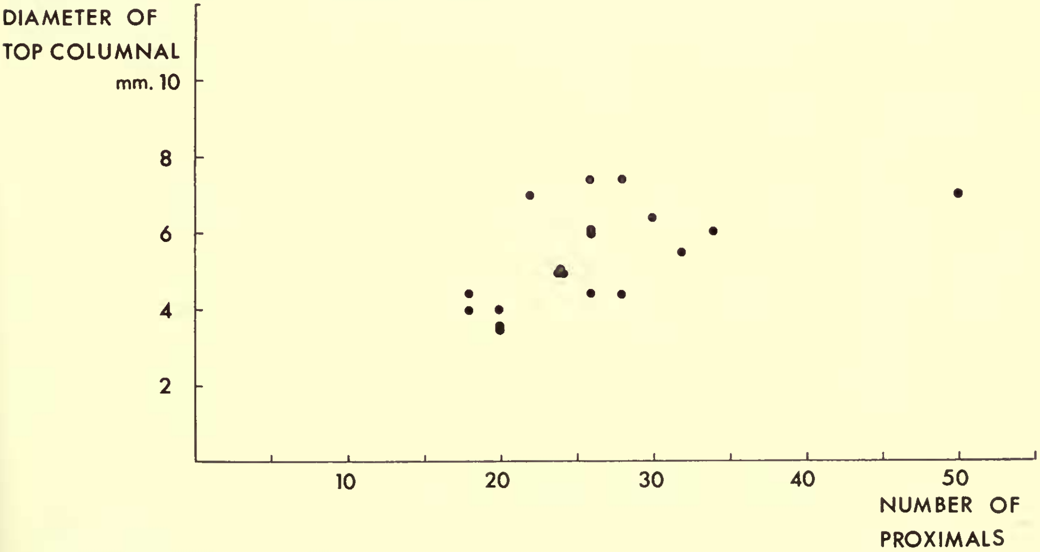


FIG. 6. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between diameter of topmost proximal columnal and number of proximal columnals.

echinoids is quite different at least initially, and so not much importance can be attached to this information.

The primary orifices of the thecae of the species described here all open across plate sutures and this is interpreted as being for mechanical convenience in growth. Enlargement of these orifices was achieved by a lack of secretion of calcite in the plates surrounding them and not by resorbtion. The slits of the pectinirhombs also grew initially by primary non-secretion of calcite. Once the slits become disjunct they could only increase in size by resorbtion. In *Lovenicystis angelini* the evidence suggests that no resorbtion occurred but apparently it did occur in *Schizocystis armata*. All the rhombs commenced as a single slit and grew by the addition of slits laterally. As the plates bearing the two half-rhombs became larger the slits became longer and beyond a certain length they became disjunct. In a fully developed rhomb all the slits are disjunct and the rims are well developed. In the present type of rhombs the spacing of slits is very constant as is their width. Internally both the dichopores and inter-dichopore spaces are approximately 0·10 mm. wide and in the majority of cases there is one dichopore and one inter-dichopore space in a width of 0·19–0·21 mm. Almost certainly this constancy of width is due to the combined thicknesses of cilated epithelium, and lengths of cilia, lining the dichopores. The fact that the inter-dichopore spaces in this type of rhomb are also of the same width indicates that these too were lined with ciliated epithelium.

c. *The Subvective System*

The ambulacra grew by the addition of flooring plates distally. In the Callocystitidae the ambulacra are wider, and the individual flooring plates thicker and wider, adorally. This suggests the last formed flooring plates were distal. There is no evidence for the addition of flooring plates adorally and it would be difficult to

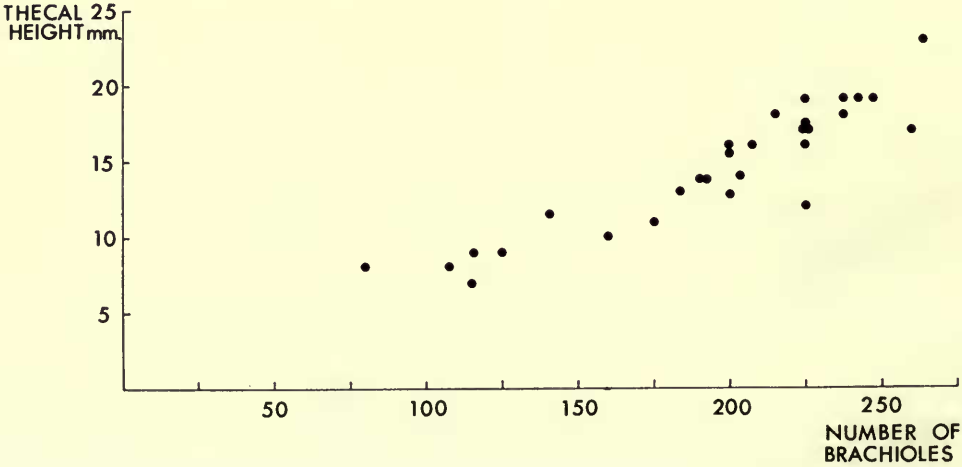


FIG. 7. *Staurocystis quadrifasciatus* (Pearce). Graphical representation of relationship between thecal height and total number of brachioles.

maintain the arrangement of brachioles in which the most adoral brachiole in each ambulacrum was branched off to the left.

Each pair of flooring plates added gave rise to another brachiole and these apparently grew rapidly as in no case have distal brachioles been found significantly shorter than the adoral ones. The brachioles grew by the addition of brachiolars distally. Kesling (1961*b*) found that the spacing of brachioles in *Pseudocrinites gordoni* Schuchert remained almost constant throughout growth and was a useful specific character. This can be confirmed for *Pseudocrinites bifasciatus* and *Staurocystis quadrifasciatus* (see Text-fig. 7) but the spacing of brachioles in *Tetracystis oblongus* and *Apiocystites pentrematoides* varies considerably. This variation is not necessarily related to growth. In species with an almost constant spacing of brachioles it is found that the spacing is slightly wider adorally, presumably due to the increased thickness of the ambulacral flooring plates.

In species with a constant spacing of brachioles, and probably in the others as well, there was considerable readjustment of the flooring plates with respect to the thecal plates throughout growth. As growth proceeded any one flooring plate migrated adorally relative to the thecal plates. Thus, for example, in *Pseudocrinities bifasciatus*, BU. Ho12 has a thecal height of 7 mm. and an estimated 12 brachioles in ambulacrum 2. Brachiole 2^{12} lay on IL2 just above the common suture with B3. In SM. A12593 (thecal height 16 mm.) brachiole 2^{12} lay on R2 just above the common suture with L3. Thus if these brachioles are homologous, as is suggested here, brachiole 2^{12} migrated across an infralateral and a lateral onto a radial plate between the two growth stages represented by these two specimens.

VII. SYSTEMATIC DESCRIPTIONS

Superfamily **GLYPTOCYSTITIDA** Bather 1899

Family **CALLOCYSTITIDAE** Bernard 1895

Subfamily **STAUROCYSTINAE** Jaekel 1899

DIAGNOSIS. A subfamily of Callocystitidae with 2–4 strongly protruding ambulacra developed on smooth bands on theca and not in shallow grooves.

In the classification which will be adopted in the forthcoming Treatise on invertebrate palaeontology (Kesling 1963) only two genera are referred to this subfamily, *Staurocystis* and *Pseudocrinites*. *Tetracystis*, which has hitherto been assigned to the Apiocystitinae, has very similar protruding ambulacra developed on smooth bands on the theca, and is here included in this subfamily on these grounds. *Prunocystites fletcheri*, the type species of *Prunocystites*, also has protruding ambulacra and so this species is included here as well.

Genus ***STAUROCYSTIS*** Haeckel 1896

Lepadocrinus of authors.

TYPE SPECIES. *Pseudocrinites quadrifasciatus* Pearce 1843.

Diagnosis. A genus of Staurocystinae with ovate theca and four ambulacra all reaching the stem, brachioles closely spaced, relatively long lateral food grooves and ambulacral cover plates frequently preserved.

At present there is only one species. Haeckel (1896*a* : 166) introduced the name *S. cruciata* but this is a nomen nudum. *S. oblongus* (Forbes) Haeckel = *Tetracystis oblongus* (Forbes), see p. 330.

Staurocystis quadrifasciatus (Pearce)

(Pl. 1, figs. 1–8; Pl. 2, figs. 1–3; Pl. 10, figs. 1–5, 12; Text-figs. 4–13)

1843*a* *Pseudocrinites quadrifasciatus* Pearce : 160.
1843*b* *Pseudocrinites quadrifasciatus* Pearce : 472.
1843*c* *Pseudocrinites quadrifasciatus* Pearce : 265.
1844 *Pseudocrinites quadricopuladigiti* Garner : 160, pl. a, fig. 14.
1848 *Pseudocrinites quadrifasciatus* Pearce ; Forbes : 498 ; pl. 13, figs. 1–13.
1854 *Pseudocrinites quadrifasciatus* Pearce ; Murchison : 216, text-fig. 37, fig. 2.
1857 *Pseudocrinus quadrifasciatus* (Pearce) Pictet : 298, pl. 99, fig. 13.
1867 *Pseudocrinites quadrifasciatus* Pearce ; Murchison : 222, 513, text-fig. 55, fig. 2.
1868 *Pseudocrinites quadrifasciatus* Pearce ; Bigsby : 26.
1873 *Pseudocrinites quadrifasciatus* Pearce ; Salter : 127.
1875 *Pseudocrinites quadrifasciatus* Pearce ; Bailey : 54, pl. 18, figs. 6*a–c*.
1876 *Pseudocrinites quadrifasciatus* Pearce ; Quenstedt : 680, pl. 113, figs. 77, 78*a–d*.
1891 *Lepadocrinus quadrifasciatus* (Pearce) Woods : 43.
1891 *Pseudocrinus quadrifasciatus* (Pearce) ; Carpenter : 7, 10.
1896*a* *Staurocystis quadrifasciatus* (Pearce) Haeckel : 134, pl. 3, figs. 1–3.
1897 *Lepadocrinus quadrifasciatus* (Pearce) ; Bather : 101, fig. 156.
1899 *Staurocystis quadrifasciatus* (Pearce) ; Jaekel : 286, text-fig. 61, pl. 14, figs. 1, 2.
1900 *Lepadocrinus quadrifasciatus* (Pearce) ; Bather : 62, text-fig. 30.
1904 *Staurocystis quadrifasciatus* (Pearce) ; Schuchert : 227.
1938 *Lepadocrinus* Spencer, pl. 2, fig. b.
1943 *Staurocystis quadrifasciatus* (Pearce) ; Bassler & Moodey : 53, 191.
1964 *Lepocrinites quadrifasciatus* (Pearce) Castell : 100, pl. 24, fig. 1.

Diagnosis. As for the genus.

Holotype. Pearce's original specimen (Bristol Museum Ca.7860) was destroyed in an air-raid on 24th November, 1940. As the species is readily recognized and there is no point of taxonomy to be settled there is no need to designate a neotype.

Material. About 140 specimens in BMNH., BU., DL., GSM., OUM., RSM., SM.

Horizon and locality. Wenlock Limestone, Middle Silurian ; Dudley (Tividale, Wren's Nest, Castle Hill) and Walsall.

Description. The theca is subovate to subquadrate and provided with four ambulacra running down the sides from the apex to the insertion of the stem. The mouth, hydropore and gonopore are apical and the anus lateral. The theca was attached to the substrate by a stem provided with a root structure.

The thecal plates are arranged according to the usual formula. The arrangement of the plates of the first four circlets is as in Text-fig. 8 and of the orals as in Text-fig. 9. The position of the ambulacra may vary slightly and four plates may surround the

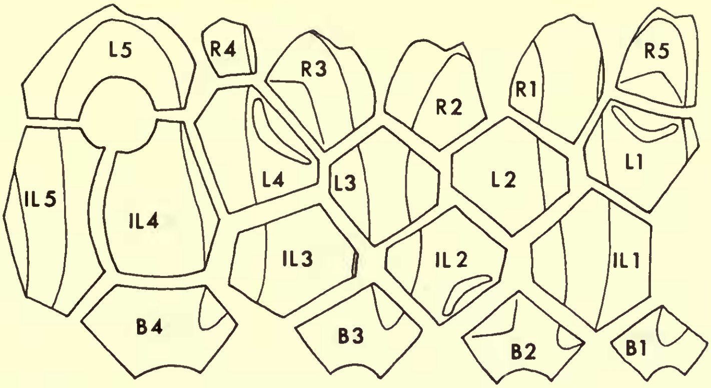


FIG. 8. *Staurocystis quadrifasciatus* (Pearce). Sketch of arrangement of thecal plates of the first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.28230.

periproct in some cases. Otherwise there is little variation in the plating arrangement. The four basal plates unite abapically to form a circular cicatrix 4·4 mm. in diameter in SM. A28230. All the plates are ornamented with radiating and concentric ridges which are often discontinuous and give the surface a malleated appearance. This ornament is only developed on the portions of the plates which do not under-lie the ambulacra. These latter portions are smooth bands on which traces of the outlines of the ambulacral flooring plates show in well preserved examples.

Three disjunct pectinirhombs are developed in all examples and are placed in the three inter-ambulacral areas which do not contain the periproct. B2 : IL2 lies in

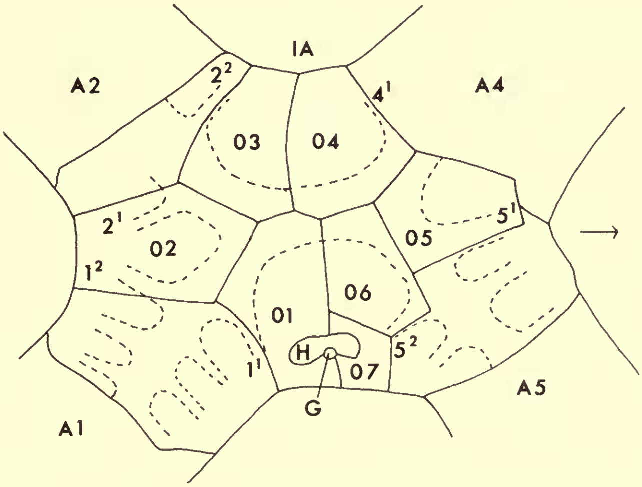


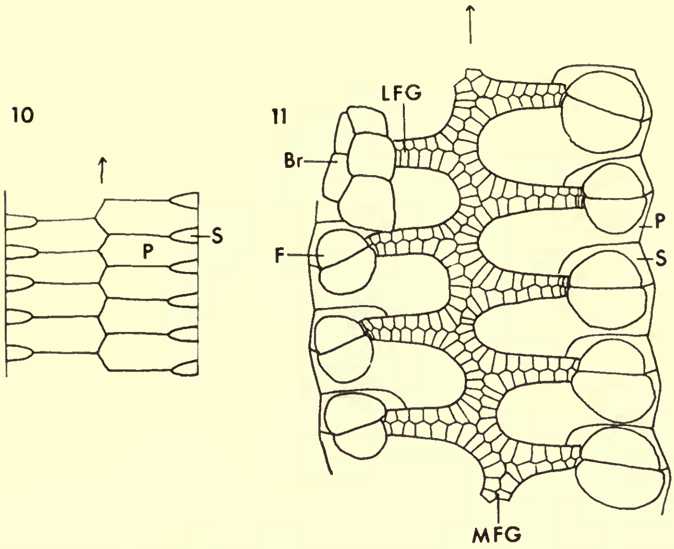
FIG. 9 *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of apical region of slightly weathered specimen, showing arrangement of orals and positions of ambulacra. AA, ambulacra ; G, gonopore ; H, hydropore ; IA, inter-ambulacrum ; OO, orals. The arrow points to the periproct. BU. Ho1.

the anterior inter-ambulacrum, L1 : R5 in the left and L4 : R3 in the right. In young specimens all or some of the pectinirhombs may be completely or partially conjunct. B2 : IL2. (BU. H069) this rhomb is depressed in outline, angular and measures 5·0 mm. by 3·7 mm. externally. B2 has an open rim while IL2 has a closed rim. There are 25 dichopores in a width of 4·35 mm. and the longest reaches 3·2 mm. The slits are 0·07 wide and reach a length of 0·9 mm. on B2 but only half that length on IL2. BMNH. E.16353–54 are two sections through this rhomb from a single specimen. Both sections are transverse and approximately parallel to the suture. In E.16353 (Pl. 10, figs. 2, 3) all the dichopores open at the surface apparently. There are 19 dichopores in a width of 3·9 mm. The outline of the section is a symmetrical triangle with the deepest dichopore at the centre. This dichopore is at least 1·2 mm. deep. The dichopores and inter-dichopore spaces are both very evenly spaced and average about 0·1 mm. in width. The dichopore walls are very thin and average about 0·015 mm. By comparison with a complete theca it is possible to infer that the section was through the half-rhomb B2. This is the only section which could pass along an ambulacrum as this one does.

E.16354 is in the same rhomb but cut nearer the suture apparently, as the deepest dichopore is deeper than in E.16353. There are only 18 dichopores in a width of 3·75 mm. They decrease in depth towards the left of the section in much the same way as in E.16353 but at a slower rate towards the right. The deepest dichopore is 1·75 mm. but the right marginal dichopore is still 1·6 mm. deep. The width of the dichopores and inter-dichopore spaces is the same however. There is an odd appearance of a membrane surrounding the entire set of dichopores internally which, under crossed nicols, coincides with a slight change in optical orientation of two calcite crystals. This could conceivably be due to the section being slightly oblique to the plate suture between B2 and IL2 and therefore passing through calcite in optical continuity with both plates. Similar "membranes" described as surrounding the hydrospires of some blastoids also coincide with optical discontinuities between calcite crystals filling the thecae (Joysey, personal communication, July, 1966).

L1 : R5. (BU. H01). This rhomb is depressed, angular and measures 3·0 mm. by 5·33 mm. externally. There are 24 or 25 dichoposes in a width of 4·8 mm. and the longest dichopore is 2·53 mm. long. The slits on R5 are regularly 0·07 mm. wide and the inter-dichopore spaces 0·125 mm. The longest slit in R5 reaches 1·07 mm. and that in L1 0·67 mm. Although the adsutural portion of the rhomb rim is not completely developed the thecal wall is more strongly raised adjacent to the slits on L1 than on R5. The slits in L1 are 0·09 mm. wide and separated by 0·107 mm.

L4 : R3. (BU. H042). It is slightly immature depressed, asymmetrical and with an angular outline. It measures 5·13 mm. by 2·93 mm. externally and has 27 dichopores in a width of 5·0 mm., the longest reaching 2·37 mm. There are 9 dichopores in the demi-rhomb adjacent to ambulacrum 4, and 18 in the demi-rhomb adjacent to ambulacrum 2. The slits in half-rhomb R3 are 0·07 mm. wide and reach a maximum length of 0·9 mm. adaxially. Those in L4 vary from 0·09–0·107 mm. in width and reach approximately 0·6 mm. in length. The slits in R3 are separated by 0·125 mm. and those in L4 by 0·09–0·107 mm. In this rhomb one or two marginal dicho-



FIGS. 10, 11. *Staurocystis quadrifasciatus* (Pearce). Fig. 10. Sketch of impression of ambulacral flooring plates on the thecal plates, near top of an ambulacrum. P, primary flooring plate ; S, secondary flooring plate. Based on specimen SM. A.28230. Fig. 11. Camera lucida drawing of part of an ambulacrum. Br, brachiole ; F, facet ; LFG, lateral food groove ; MFG, main food groove ; P and S as in Fig. 10. The arrows point to the mouth. Based on specimen SM. A.11156.

pores are conjunct and the adsutural rim is virtually undeveloped. However BMNH. 47908 shows a fully developed rhomb which is even more asymmetrical and has a complete closed rim on L4 and only an absutural rim on R3. BMNH. 57385 is particularly interesting as the demi-rhomb adjacent to ambulacrum 4 is only partly formed and apparently its growth was inhibited by the presence of the ambulacrum (see Pl. 2, fig. 2).

The mouth has not been directly observed but presumably lay apically at the confluence of the four ambulacra (see Text-fig. 4). It was surrounded by 7 orals arranged as in Text-fig. 9. The ambulacra were developed on broad bands on the theca. These bands are 4·0 mm. wide at the apex in SM. A28230 and taper very gradually towards the tips. The primary ambulacral flooring plates were very thin and narrow and the secondary flooring plates were very small in comparison and did not reach the ambulacral mid-line (see Text-fig. 10). The brachiole facets are small kidney-shaped areas and are in contact with each other. Their spacing appears to have been almost constant throughout growth. The average of ten measurements, taken from five specimens (one near the tip and one near the mouth for each) was 5 brachioles in 3·59 mm. The variation was from 5 in 3·2 mm. to 5 in 3·8 mm. The constancy of this feature during growth is also indicated to a certain extent by Text-fig. 7. The main and lateral food grooves of the ambulacrum are provided with cover plates which apparently did not articulate with the flooring plates in life and formed a permanent roof over the food groove. They are very narrow plates, about

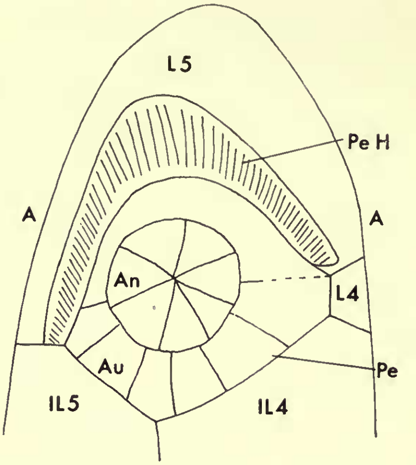


FIG. 12. *Staurocystis quadrifasciatus* (Pearce). Camera lucida drawing of area around periproct, showing four plates surrounding the periproct. AA, ambulacra; An, anal pyramid; Au, auxiliary circlet; ILL, infralaterals; LL, laterals; Pe, periproct (comprising anal pyramid and auxiliary circlet); Pe.H, periproct hood. Cf. Pl. 1, fig. 7; Pl. 2, fig. 3. BMNH. 48197.

half the width shown in Text-fig. 11, and are apparently unornamented. Between the lateral food grooves the primary flooring plates are ornamented with a large central tubercle and occasionally another smaller tubercle close to the main food groove (see Pl. 2, fig. 3). The brachioles are composed of about 3 dozen regularly alternating brachiolars and are about 6–8 mm. long. They have a central straight food groove, about 0·2 mm. wide and provided with cover plates. There are three cover plates per brachiolar. In BMNH. E.7512 the brachioles are 0·7 mm. wide at the base and taper gradually throughout their length to 0·4 mm. near the tips.

The periproct is surrounded by three thecal plates in most cases. These are, in increasing order of contribution to the border: IL5, IL4, L5. Occasionally L4 also reaches the periproct and contributes to a very small portion of the border. L5 frequently surrounds half the periproct and is provided with a special structure immediately adoral to the periproct here termed the *periproct hood* (Text-fig. 12). The periproct may be circular or bell-shaped and contains an anal pyramid reaching 3 mm. in diameter and composed of 5–7 anals. The anal pyramid is surrounded by a circlet of auxiliaries which may be open or closed and consists of about 9 plates. Both the anals and auxiliaries may have slightly raised margins.

The gonopore and hydropore are apical and shared by O1 and O7, as is usual. The gonopore is a small circular opening 0·25 mm. in diameter in BU. Ho1. Adoral to it and slightly curved around it is the hydropore which is provided with a rim. BMNH. 57381, which has the oral area ground down, shows an embayment in the internal margin of the thecal wall just below the point of emergence of these orifices (see Text-fig. 13).

The stem is very variable in length and relative proportions of the proximal and

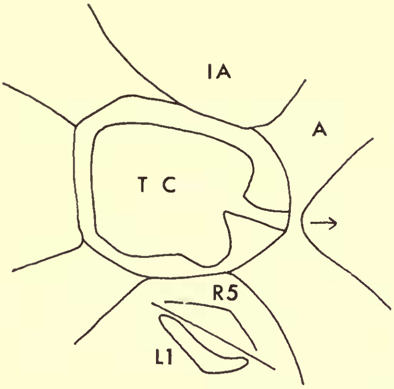


Fig. 13. *Staurocystis quadrifasciatus* (Pearce). Sketch of apical region ground down. Note embayment above rhomb L1 : R5 at position of gonopore and hydropore. A, ambulacrum ; IA, inter-ambulacrum ; TC, thecal cavity. The arrow points to the periproct. BMNH. 57381.

distal portions (see Pl. 10, figs. 1, 4, 5). The proximal portion tapers rapidly and the outer proximals have a smooth external flange. The distal portion is almost without any taper and the alternation of the distals is indistinct after the first few pairs. BMNH. E.7553, 38696 and BU. H019 show distinct branched root structures.

Remarks. This is the commonest species from the Wenlock Limestone and was gregarious. A slab of Wenlock Limestone in the Geological Survey & Museum, London, has the remains of 8 specimens preserved on it and one in the Dudley Library has remains of 10 specimens. Another slab, in the Sedgwick Museum, has 2 specimens of this species and one of *Tetracystis oblongus* (Forbes) on it. It is interesting that despite the complexity of the food collecting apparatus in this genus, it is confined to the Wenlock Limestone, whereas *Tetracystis* and *Pseudocrinites* are more widely distributed and survived until the Devonian.

Genus ***PSEUDOCRINITES*** Pearce 1843

Type species. *Pseudocrinites bifasciatus* Pearce 1843, by designation of Haeckel (1896*a* : 135).

Diagnosis. A genus of Staurocystinae with lens-like, biconvex theca ; with two ambulacra. Modified from Kesling (1963 : 111).

Ten species of *Pseudocrinites* have so far been described in addition to the one Schuchert described as *Trimerocystis peculiaris*, an abnormal individual which had three ambulacra instead of the usual two. Kesling (1961*a* : 257) considered *P. abnormalis* Schuchert and *T. peculiaris* Schuchert to be synonymous with *Pseudocrinites gordoni* Schuchert, and I believe that *Pseudocrinites magnificus* Forbes is probably a very large individual of *P. bifasciatus* Pearce. This reduces the number of species to 8 and it might be possible to reduce it even further if a comprehensive study of the American species were undertaken. One new species is described here based on two specimens from the Holcroft collection (BU). Both differ considerably from *P. bifasciatus* but quite closely resemble the American species *P. perdewi* Schuchert.

REGIONAL DISTRIBUTION. England : Dudley, Walsall, Sedgley. United States : W. Virginia, Pennsylvania and Maryland.

STRATIGRAPHIC RANGE. Wenlock Limestone (Middle Silurian) to Manlius Formation (Devonian, Gedinnian).

Pseudocrinites bifasciatus Pearce

(Pl. 2, figs. 4–8 ; Pl. 3, figs. 2–6 ; Pl. 10, figs. 7, 8 ; Text-figs. 14–19)

1843*a* *Pseudocrinites bifasciatus* Pearce : 160.
1843*b* *Pseudocrinites bifasciatus* Pearce : 472.
1843*c* *Pseudocrinites bifasciatus* Pearce : 265.
1844 *Pseudocrinites bicopuladigiti* Garner : 160, pl. A, figs. 8–13.
1848 *Pseudocrinites bifasciatus* Pearce ; Forbes : 496, pl. 11, figs. 1–7.
1848 *Pseudocrinites magnificus* Forbes : 497, pl. 12, figs. 1–4.
1854 *Pseudocrinites bifasciatus* Pearce ; Murchison : 216.
1854 *Pseudocrinites magnificus* Forbes ; Murchison : 216, text-fig. 37, fig. 1.
1857 *Pseudocrinus bifasciatus* (Pearce) Pictet ; 298, pl. 99, fig. 12.
1857 *Pseudocrinus magnificus* (Forbes) Pictet : 298.
1867 *Pseudocrinites bifasciatus* Pearce ; Murchison : 222, 513.
1867 *Pseudocrinites magnificus* Forbes ; Murchison : 222, 513, text-fig. 55, fig. 1.
1868 *Pseudocrinites bicopuladigiti* Garner ; Bigsby : 26.
1868 *Pseudocrinites bifasciatus* Pearce ; Bigsby : 26.
1868 *Pseudocrinites magnificus* Forbes ; Bigsby : 26.
1873 *Pseudocrinites bifasciatus* Pearce ; Salter : 127, 2 figs.
1876 *Pseudocrinites bifasciatus* Pearce ; Quenstedt : 678, pl. 113, figs. 74 (3 figs.), 75.
1891 *Lepadocrinus bifasciatus* (Pearce) Woods : 43.
1891 *Pseudocrinus bifasciatus* (Pearce) ; Carpenter : 7, 10.
1895 *Pseudocrinus bifasciatus* (Pearce) ; Bernard : 206, text-fig. 73*c*.
?1896 *Pseudocrinus*, Haeckel : 401.
1896*a* *Pseudocrinites bifasciatus* Pearce ; Haeckel : 135, pl. 3, figs. 25, 26.
1896*a* *Pseudocrinites magnificus* Forbes ; Haeckel : 136.
1899 *Pseudocrinites bifasciatus* Pearce ; Jaekel : 285, pl. 14, fig. 3, text-fig. 60.
1899 *Pseudocrinites magnificus* Forbes ; Jaekel : 285, pl. 14, fig. 4.
1900 *Pseudocrinus* Bather : 62, text-fig. 29.
1904 *Pseudocrinites bifasciatus* Pearce ; Schuchert : 227, 229.
1904 *Pseudocrinites magnificus* Forbes ; Schuchert : 229.
1943 *Pseudocrinites bifasciatus* Pearce ; Bassler & Moodey : 53, 185.
1943 *Pseudocrinites magnificus* Forbes ; Bassler & Moodey : 53, 185.

DIAGNOSIS. A *Pseudocrinites* with circular outline to theca ; very broad ambulacra reaching stem ; periproct composed of anal pyramid and complete circlet of auxiliaries ; thecal plates sculptured with coarse irregular ridges giving theca a malleated appearance.

HOLOTYPE. Pearce's original specimen (Bristol Museum Ca.7862) was destroyed in an air-raid on 24th November, 1940. Again as this species is readily recognized and there is no point of taxonomy to be settled no neotype is designated.

Material. About 35 specimens in BMNH., BU., DL., GSM., OUM., RSM., SM.

Horizon and locality. Wenlock Limestone, Middle Silurian ; Dudley (Wren's Nest and Castle Hill).

Before describing the species it is necessary to settle the synonymy between *P. bifasciatus* Pearce and *P. magnificus* Forbes.

There is a constant number of brachioles per unit length in the ambulacra of *Staurocystis quadrifasciatus* and, according to Kesling (1961*a*), in *Pseudocrinites gordoni* Schuchert. If this holds true for *P. bifasciatus* there will be a linear relationship between thecal diameter and the total number of brachioles. Text-fig. 14 clearly shows that this is so and that *P. magnificus* falls very close to the predicted value for a large *P. bifasciatus*. This is a particularly important point for in his original description Forbes (1848 : 497) stated that " the arms extend completely down the sides, and are remarkable for the great number of fingers [brachioles] on each, being no fewer than 34. [Forbes only counted the brachioles on one side of each ambulacrum.] They are much more closely packed, longer, slenderer, and apparently more flexible than in the last species. [*P. bifasciatus*] ". The number of brachioles was the main point distinguishing the two species and since there is in fact very little real difference they must be considered synonymous.

Description. The theca is circular in outline, biconvex and lens-like. There are two ambulacra running around the periphery of the theca and usually reaching the

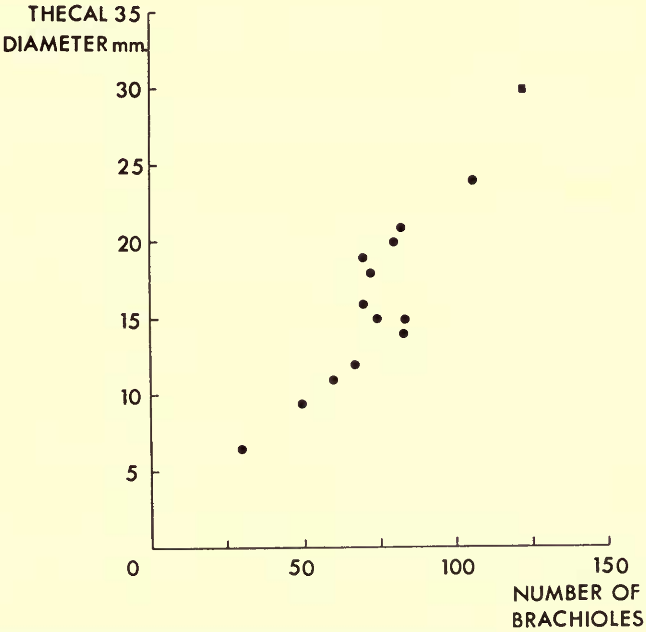


Fig. 14. Graphical representation of relationship between diameter and total number of brachioles in *Pseudocrinites bifasciatus* Pearce and *P. magnificus* Forbes. The square dot represents the holotype of *P. magnificus*.

stem. The mouth, gonopore and hydropore are apical and the anus lateral. The anus and rhomb L4 : R3 were in one lateral face, the periproctal face, while rhombs B2 : IL2 and L1 : R5 were in the other face. The gonopore and hydropore are therefore in this face which is referred to as the gonal face.

The thecal plates of the first four circlets are arranged in the usual order (see Text-fig. 15). The exact positions of the ambulacra may vary slightly but otherwise there is very little variation. As far as it is possible to determine the arrangement of the visible portions of the orals is as in Text-fig. 16 but they extended over a larger area beneath the ambulacra. The four basals combine abapically to form an oval cicatrix 5·5 mm. by 5·0 mm. in SM. A12593. All the plates are ornamented with irregular and discontinuous radiating and concentric ridges very much like those of *Staurocystis*. The portions of the thecal plates underlying the ambulacra bear the impressions of the flooring plates. These are much less closely packed than in *Staurocystis* (see Text-fig. 18).

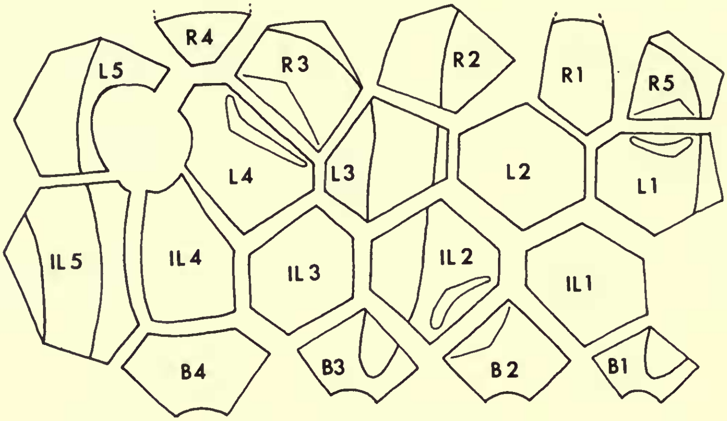


FIG. 15. *Pseudocrinites bifasciatus* Pearce. Sketch of arrangement of thecal plates of first four circlets. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. Based on specimen SM. A.12593.

Three disjunct pectinirhombs are present, of these B2 : IL2 and L1 : R5 are about the same size and L4 : R3 is distinctly larger.

B2 : IL2. (SM. A12593). This rhomb is depressed, angular and almost perfectly symmetrical. It measures 4·7 mm. by 3·8 mm. externally and has 22 dichopores in a width of 3·9 mm., the longest reaching 3·0 mm. The slits in B2 are 0·07 mm. wide and separated by 0·125 mm. They reach a maximum length adaxially of 0·87 mm. Those in IL2 are 0·107 mm. wide and separated by 0·09 mm. and reach a maximum length of 0·62 mm. The closed rim on IL2 protrudes about 0·4 mm. from the general surface of the plate.

L1 : R5. (SM. A10192). This rhomb is depressed, more or less equal and symmetrical. It measures 4·35 mm. by 3·65 mm. externally and has 20 dichopores in a width of 3·35 mm., the longest reaching approximately 3·0 mm. The slits in R5 are

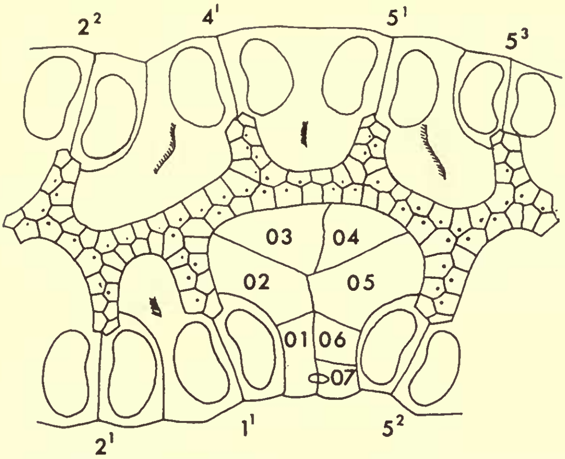
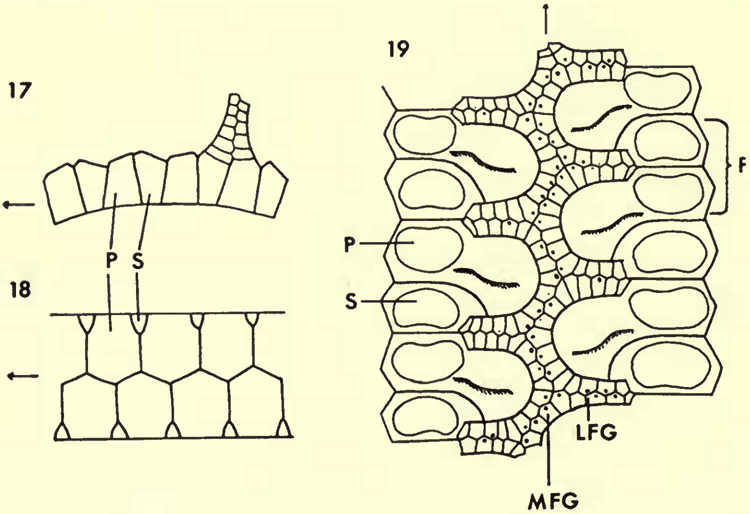


FIG. 16. *Pseudocrinites bifasciatus* Pearce. Sketch of apical region, showing arrangement of the ambulacra, interpretation of the brachioles and the exposed portions of the oral plates. OO, orals. SM. A.10192.

0·07 mm. wide and separated by 0·125 mm. The longest reaches 1·1 mm. Unfortunately the slits in L1 are obscured by matrix but could not have exceeded 0·65 mm. in length. L1 has a closed rim extending about 0·4 mm. from the level of the plate surface.

L4 : R3. (SM. A12593). This is depressed, very asymmetrical and angular. It measures 6·0 mm. by 3·0 mm. approximately (it is slightly damaged). There are 32 dichopores in a width of 6·0 mm. and the longest reaches approximately 2·35 mm. The slits in R3 are 0·07 mm. wide and separated by 0·125 mm., the longest reaching 0·87 mm. Again unfortunately those in L4 are obscured by matrix but could not have exceeded 0·53 mm. in length.

The mouth lay apically between facets 4^1 and 1^1 and shows as a narrow curved slit in BMNH. 47833. This specimen shows the internal view of the gonal face and apex. There is a slight groove internally in R5 below the gonopore and the hydropore. There are two broad ambulacra which coalesce at the apex and usually reach the stem. They are 5 mm. wide at the apex in SM. A12593 and taper gradually to about 3 mm. at their rounded tips. The primary flooring plates are not as thin as those of *Staurocystis* resulting in a more distant spacing of the brachioles. The ambulacra are more prominent than in *Staurocystis* and reach a height of 2 mm. in BMNH. 40189. The brachiole facets are kidney-shaped areas which are quite prominent and set at an angle of about 45 degrees to the line of the ambulacrum. The spacing of the facets appears to be constant throughout growth and a specific character. The average of ten measurements was 4 brachioles in 5·3 mm. with maximum and minimum of 4 in 6·0 mm. and 4 in 4·9 mm. These measurements were taken from thecae varying in diameter from 11 mm. to 24 mm. The main and lateral food grooves of the ambulacra are provided with cover plates which are much broader than those of *Staurocystis* or *Pseudocrinites pyriformis* sp. nov. and are frequently ornamented with tubercles (see Text-fig. 19). Apparently these cover plates formed a permanent roof over the food grooves. Between lateral food grooves the primary flooring plates are ornamented with a slightly sinuous ridge. The brachioles taper very rapidly near the base so that although the facets are almost in contact adjacent brachioles are widely separated. They are composed of about 24 to 28 brachiolars and reach a length of about 6–6·5 mm. Basally they are 1 mm. wide and taper rapidly to start with, then gradually to about 0·5 mm. at the tips. The brachioles are provided with cover plates which are 3 or 4 times as numerous as the brachiolars. Most of these features are well preserved on BMNH. E.29068.



Figs. 17–19 *Pseudocrinites bifasciatus* Pearce. Fig. 17. Sketch of side of an ambulacrum, showing primary and secondary flooring plates and a brachiole tapering rapidly at the base. Fig. 18. Sketch of impression of ambulacral flooring plates on the thecal plates. Fig. 19. Sketch of part of an ambulacrum. F, facet ; LFG, lateral food groove ; MFG, main food groove ; P, primary flooring plate ; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.10192.

The periproct is surrounded by four plates. In increasing order of contribution to the border these are : IL5, IL4, L4, L5, the latter contributing about one-third the total. There is no periproct hood in L5. The periproct is covered by an anal pyramid, composed of 5 or 6 anals and up to 2·65 mm. in diameter, and an auxiliary circlet which is always complete and composed of 10 plates in BMNH. E.29068 and 40198. Both anals and auxiliaries are apparently unornamented.

The gonopore and hydropore are apical and shared by O1 and O7. The gonopore is a small circular opening 0·25 mm. in diameter in BU. Ho12 which is a very immature specimen. The hydropore is oblong in this specimen and about twice the size of the gonopore. No gonals have been observed. As previously mentioned, there is a groove in R5, which corresponds in position to the embayment seen in *Staurocystis*, below the position of these two orifices.

The stem is composed of the usual proximal and distal portions and, in BMNH. 40189, has a root structure. The outer proximals are provided with a smooth external flange and the distals are not clearly recognizable as large and small throughout most of the length. In BMNH. 40189 there are 14 outer proximals and about 21 distals of which the first six are in distinct pairs of large and small. The stem is about 27 mm. long.

REMARKS. Schuchert (1904 : 228–229) grouped the American species of this genus into three groups :

P. gordoni group. Thecal outline circular, ambulacra reaching the stem, auxiliary circlet complete.

P. clarki group. Thecal outline elongate, ambulacra reaching the stem, auxiliary circlet incomplete.

P. perdewi group. Thecal outline pyriform, ambulacra not reaching the stem, auxiliary circlet complete.

Schuchert assigned *P. bifasciatus* and *P. magnificus* to the *gordoni* group and this seems to be correct. However, some doubt may be cast as to the distinctness of the first two groups as some examples of *P. bifasciatus* seem to have elongate thecae, and the nature of the auxiliary circlet is known to vary within a single species in other genera of Staurocystinae. The third group, that of *P. perdewi*, is apparently quite distinct from the other two and the next species described in this paper belongs in it. There may be some grounds for separating these two species from the others subgenerically but without a thorough re-examination of the American species this would seem a hasty action.

Pseudocrinites pyriformis sp. nov.

(Pl. 3, figs. 1, 7 ; Pl. 4, figs. 1–5 ; Pl. 5, fig. 1 ; Text-figs. 20, 21)

DIAGNOSIS. A *Pseudocrinites* with pyriform outline to the theca ; broad ambulacra extending only half way down the sides ; thecal plates showing coarse irregular sculpture adorally and fine irregular sculpture associated with fine radiating ridges aborally.

HOLOTYPE. BU. H010.

MATERIAL. In addition to the holotype, paratype BU. H011.

HORIZON and LOCALITY. Sedgley (Aymestry) Limestone, Upper Silurian ; Sedgley, Staffs.

DESCRIPTION. The theca is pyriform in outline and bilaterally compressed with ambulacra in a broad band running across the top of the theca and extending about half way down the sides. The mouth, gonopore and hydropore are apical and the anus lateral. Rhombs B2 : IL2 and L1 : R5 are in the gonal face, and the periproct and rhomb L4 : R3 in the periproctal face. The theca was provided with a stem.

The arrangement of the thecal plates of the first four circlets is as in Text-fig. 20. The arrangement of the orals is unknown. Neither of the specimens available shows all the thecal plates, and those plates shown in dashed outline are not clearly visible.

In BU. Ho11 the ambulacra extend a little further down the theca and encroach upon ILL2 and 5, but this seems to be the only difference. Where the plates are not covered by the ambulacra they have a very distinctive ornament. In the adoral half of the theca this is of very irregular ridges and pits accompanied by fine tubercles throughout. Aborally however the ornament is of much finer irregular ridges, which do not protrude as far from the general surface, fine tubercles and some fine radiating ridges. In the holotype the basal plates appear to be almost smooth but this is partly due to weathering. The basals unite abapically to form a cicatrix 7·3 mm. by 6·0 mm., but as this part of the theca is slightly crushed the cicatrix may have been circular originally.

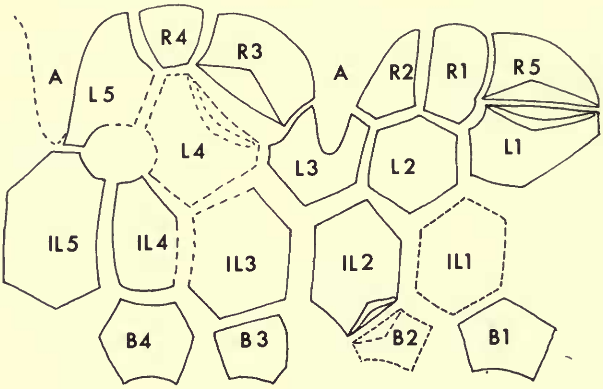


FIG. 20. *Pseudocrinites pyriformis* sp. nov. Sketch of arrangement of thecal plates of first four circlets. AA, ambulacra; BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. The plates indicated by a dashed outline are not clearly visible. Based on specimen BU. Ho10.

The usual three disjunct pectinirhombs are developed. Both specimens show L1 : R5 clearly, the holotype shows half-rhomb R3, and neither show B2 : IL2 clearly although part of it is visible.

B2 : IL2. Part of IL2 shows in the holotype. It has a closed rim and shows 18 slits in a width of 4·2 mm., the longest reaching 1·0 mm. The slits are 0·161 mm. wide and separated by 0·107 mm. which is unusually wide.

L1 : R5. (Holotype). This is very depressed, more or less angular and symmetrical. It measures 12·3 mm. by 5·7 mm. externally and has 43 dichopores in a width of 11·7 mm., the longest reaching 4·0 mm. The slits in R5 are 0·107 mm. wide and separated by 0·125 mm. They reach a length of 2·0 mm. Those in L1 are 0·143 mm. wide and separated by 0·09 mm. They reach a maximum length adaxially of 0·95 mm. Due to the development of the closed rim around this half-rhomb these slits open on a surface sloping away from the suture at an angle approaching 45 degrees (see Pl. 4, fig. 2).

(BU. Ho11). This rhomb is much the same and has about 40 dichopores in a width of 12 mm. approximately. The slits in R5 reach a length of 2·0 mm. while those in L1 reach 1·0 mm. The slits are again narrower, and consequently more widely separated, in R5 than in L1.

L4 : R3. (Holotype). This rhomb is only half visible and shows 45 dichopores in R3 in a width of 12·0 mm. but there were probably a few more which are now hidden by matrix. It is asymmetrical, there being 18 dichopores in the demi-rhomb adjacent to the periproct and therefore at least 27 in the other demi-rhomb. The slits in R3 are 0·107 mm. wide and separated by 0·125 mm. The longest is 2·33 mm. long.

The mouth has not been directly observed but presumably lay between facets 1^1 and 4^1 as in *P. bifasciatus*. The ambulacra are developed on broad bands which taper relatively rapidly. They are 7 mm. wide apically and taper to about half that just before their rounded tips. Apically the ambulacral flooring plates are 3·5 mm. high in the holotype and 4·0 mm. in Ho11. There are 14 facets in ambulacrum 5 and 16 in ambulacrum 2 of Ho10, the corresponding figures for Ho11 being 20 and 24. The arrangement of the flooring plates is much the same as in *P. bifasciatus* but the brachioles are much more widely spaced. The average of four measurements was 4 facets in 10·4 mm. with maximum and minimum distances of 10·0 and 11·0 mm. These are almost twice the distances for *P. bifasciatus*. The facets are large kidney-shaped areas which are almost planar. The main and lateral food grooves are provided with highly ornamented cover plates which are relatively long and narrow. They have the same general proportions as those of *Staurocystis* but differ in being much larger and in being covered with strongly raised ridges. Between the lateral food grooves the primary flooring plates are highly ornamented with raised tubercles, and both types of flooring plates are ornamented with ridges laterally. The main food grooves are provided with a narrow ledge on which the cover plates rested in life. The lateral food grooves were relatively short. The brachioles are composed of alternating brachiolars ornamented with tubercles and ridges. The penultimate

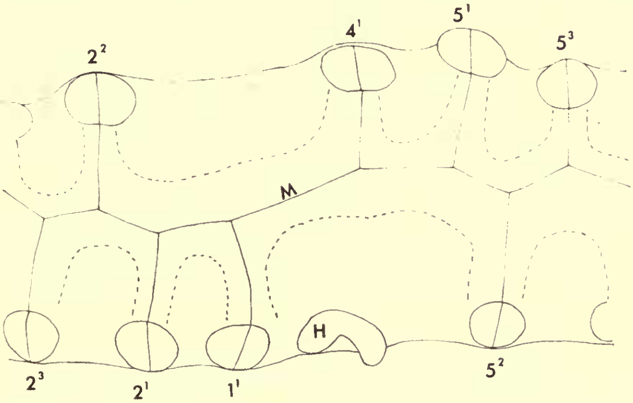


FIG. 21. *Pseudocrinites pyriformis* sp. nov. Camera lucida drawing of apical region. H, hydropore ; M, approximate position of mouth. Cf. Text-figs. 4, 16. Based on specimen BU. Ho10.

brachiole in ambulacrum 5 of Ho11 is 9·35 mm. long and has 22 brachiolars in this distance. It is incomplete however. The terminal brachiole apparently exceeds 12 mm. in length and this too is incomplete. The penultimate one tapers from 1·45 mm. wide at the base to 0·65 mm. where it is broken off. The cover plates are apparently ridged and about 2–3 per brachiolar.

The periproct is probably surrounded by four plates but cannot be seen completely in either specimen. Parts of the anal pyramid and auxiliary circlet can be made out in the holotype but the total number of plates in each is unknown. In Ho11 the auxiliaries were ornamented with ridges. There is no periproct hood in L5.

The gonopore and hydropore lay apically presumably across the common suture of O1 and O7. The gonopore is small, circular and provided with a pyramid of gonals, of which 2 can be seen in the holotype. It is 0·35 mm. wide in the holotype and 0·65 mm. wide in Ho11. The hydropore is curved around the gonopore adapically and provided with a conspicuous rim bearing ridges externally. It is 1·85 mm. wide in the holotype and 3·45 mm. wide in Ho11.

21·5 mm. of the proximal stem is preserved in the holotype. It tapers from 7·0 mm. to 4·5 mm. in this distance and there are 26 outer proximals each provided with an external flange that has tubercles developed on the less weathered portions.

REMARKS. This species is quite distinct from the preceding but closely resembles *P. perdewi* Schuchert. It differs from the latter species in the brachiole and dichopore spacing, in having more prominent ambulacra and less prominent rhombs. The holotype has 45 dichopores in L4 : R3 whereas a specimen of *P. perdewi* of about the same dimensions would have about 70 dichopores in the same rhomb. The ornamentation of the plates of the two species is also quite different. As a general rule the British species of Staurocystinae seem to have more prominent ambulacra and less well developed rhombs than their American counterparts.

Genus ***TETRACYSTIS*** Schuchert 1904

TYPE SPECIES. *Tetracystis chrysalis* Schuchert 1904.

DIAGNOSIS. A genus of Staurocystinae with four protruding ambulacra all reaching the stem ; relatively widely spaced brachioles ; wide main food groove and short lateral food grooves ; some secondary ambulacral flooring plates reaching ambulacral mid-suture ; ambulacral cover plates rarely preserved.

Hitherto the genus *Tetracystis* has been assigned to the subfamily Apiocystitinae. Kesling (1963 : 108) lists among the characters of the Staurocystinae that the ambulacra are strongly protuberant. In both genera attributed by Kesling to the Staurocystinae this is due to the ambulacra being developed on smooth bands on the thecal plates and not in shallow grooves as in the Apiocystitinae. In both these respects *Tetracystis* resembles *Staurocystis* and *Pseudocrinites* and is therefore included in the Staurocystinae.

The specimens described by Forbes as *Pseudocrinites oblongus* apparently belong to this genus. They have four ambulacra three pectinirhombs and four plates bordering the periproct. In Regnéll's scheme for the Apiocystitinae (Regnéll

1945 : 91) there are only three genera which fall into this category. These are *Lovenicystis* Regnéll 1945, *Jaekelocystis* Schuchert 1903 and *Tetracystis* Schuchert 1904. The present specimens differ from *Lovenicystis* in having all the ambulacra reaching the column and from *Jaekelocystis* in having angular pectinirhombs in which one half-rhomb is not reduced to a spout-like pore. They agree with *Tetracystis* in these respects and also in the nature of the ambulacra which has caused their removal to the Staurocystinae. There are only three other species known at present, *T. chrysalis* Schuchert, *T. bifarius* Amsden and *T. fenestratus* (Troost). The British species appears to differ from all three in having more prominent ambulacra.

REGIONAL DISTRIBUTION. England : Dudley ; United States : Tennessee and W. Virginia.

STRATIGRAPHICAL RANGE. Middle Silurian to Basal Devonian.

Tetracystis oblongus (Forbes) 1848

(Pl. 5, figs. 2–7, 11–13 ; Pl. 10, figs. 6, 13 ; Text-figs. 22–25)

1848 *Pseudocrinites oblongus* Forbes : 499, pl. 14, figs. 1–14.
1854 *Pseudocrinites oblongus* Forbes ; Murchison : 217.
1857 *Pseudocrinus oblongus* (Forbes) Pictet : 298.
1867 *Pseudocrinites oblongus* Forbes ; Murchison : 222, 513.
1868 *Pseudocrinites oblongus* Forbes ; Bigsby : 26.
1873 *Pseudocrinites oblongus* Forbes ; Salter : 127.
1876 *Pseudocrinites oblongus* Forbes ; Quenstedt, pl. 113, fig. 79, (3 figs.).
1891 *Pseudocrinus oblongus* (Forbes) ; Carpenter : 10.
1896*a* *Staurocystis oblongus* (Forbes) Haeckel : 134.
1899 *Apiocystites oblongus* (Forbes) Jaekel : 282.
1900 *Lepadocrinus oblongus* (Forbes) Bather : 62.
1943 *Lepocrinites oblongus* (Forbes) Bassler & Moodey : 52, 173.

DIAGNOSIS. A *Tetracystis* with broad, prominent ambulacra ; up to 30 brachioles per ambulacrum and up to 30 dichopores per rhomb ; periproct relatively depressed.

LECTOTYPE. Forbes did not designate a type but the specimens he examined were in the Fletcher and Gray collections. Among the specimens in the Fletcher collection is the original of Forbes' pl. 14, fig. 1 (SM. A10140), here selected as lectotype.

MATERIAL. In addition to the lectotype, 9 specimens in BMNH. GSM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs.

DESCRIPTION. The theca is subquadrate with four ambulacra reaching the stem. The mouth, gonopore and hydropore are apical and the anus lateral. No complete stem has been seen.

The arrangement of the thecal plates of the first four circlets is shown in Text-fig. 22. Very few specimens are known and there is little variation among them. The four basal plates unite abapically to form a circular cicatrix 4 mm. in diameter in the lectotype. The thecal plates are ornamented with irregular radiating and concentric ridges which are often discontinuous and strongly resemble the ornamentation in *Staurocystis* and *Pseudocrinites bifasciatus*. Beneath the ambulacra the traces of the

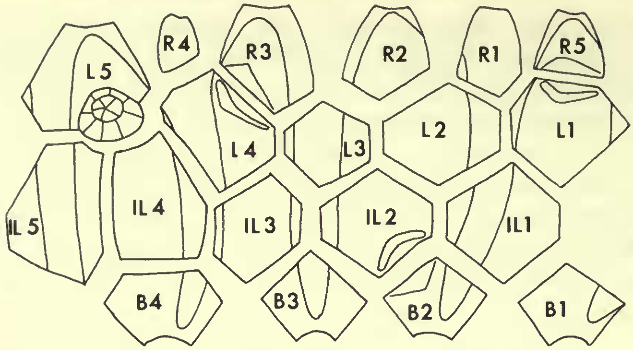
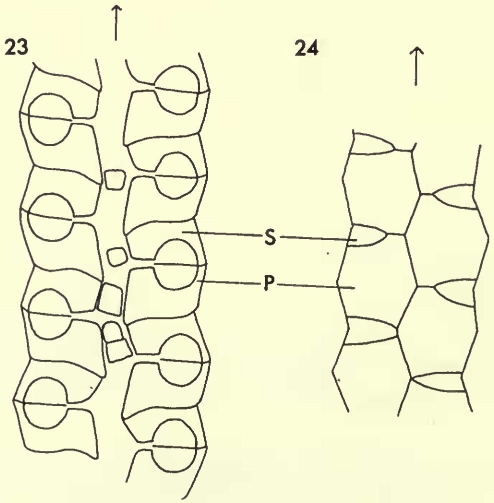


FIG. 22. *Tetracystis oblongus* (Forbes). Sketch of arrangement of thecal plates of first four circlets. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. Based on specimen SM. A.10140.

ambulacral flooring plates can be made out. As far as can be determined from BMNH. 57411 there were 7 orals arranged in much the same way as in *Staurocystis*.

The usual three disjunct pectinirhombs are present. They are all angular and depressed in outline.

B2 : IL2 (Lectotype). This is 3·15 mm. by 2·15 mm. and has 19 dichopores in a width of 2·9 mm. The longest dichopore is 1·8 mm. The slits in IL2 are obscured by matrix, those in B2 are up to 0·054 mm. wide and separated by 0·125 mm. IL2 is provided with a closed rim.



FIGS. 23, 24. *Tetracystis oblongus* (Forbes). Fig. 23. Sketch of part of an abulacrum. Fig. 24. Sketch of impression of ambulacral flooring plates on the thecal plates. P, primary flooring plate; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.10140.

L1 : R5 (Lectotype). This is 3·75 mm. by 2·75 mm. externally and has 23 dichopores in a width of 3·6 mm. and the longest dichopore is 2·27 mm. The slits in both half-rhombs are 0·07 mm. wide, and separated by 0·125 mm. Those of L1 reach 0·54 mm. in length while those in R5 reach 1·0 mm.

L4 : R3 (Lectotype). The rhomb measures 4·8 mm. by 3·0 mm. and is asymmetrical, possibly due to the proximity of ambulacrum 4. There are 28 dichopores, all of which are disjunct, in a width of 4·45 mm. and the longest is 2·4 mm. The slits in L4 are 0·07 mm. wide and separated by 0·107 mm. while those the longest reaching 0·67 mm. Those in R3 are only 0·055–0·06 mm. wide and separated by 0·1 mm. The longest is 0·95 mm. long.

The mouth was apical and slit-like (BMNH. 57411) and apparently surrounded by 7 orals. The four ambulacra meet in the oral area and the first formed facets are on the left as in other species of Staurocystinae (see Text-fig. 25). The four ambulacra are developed on relatively narrow bands which, contrary to Forbes' statement, hardly taper at all. They are 2·5 mm. wide apically and still 2·0 mm. wide near their tips. They are much more conspicuous in this species than in the American species. The arrangement of the ambulacral flooring plates is shown in Text-fig. 24. The secondary flooring plates are much larger relatively than in *Staurocystis* or *Pseudocrinites* and quite frequently reach the ambulacral mid line. The brachiole facets are rather inconspicuous but slightly raised and the lateral food grooves are relatively short. Both the lateral and main food grooves were covered with ambulacral cover plates which were subquadrate and unornamented. Apparently the primary flooring plates were also unornamented between the lateral food grooves. The spacing of the brachiole facets varies within much wider limits than in the previous two genera. The average of 8 measurements was 4 brachioles in 5·73 mm. but varied from 4 in 4·67 mm. to 4 in 7·0 mm. This may vary within a single specimen and is not directly associated with growth as the largest theca had an intermediate value. The brachioles are narrow, being 0·7 mm. wide basally in SM. A12603, and they taper gradually. No complete brachiole has been seen but 20 brachiolars are preserved in some brachioles on SM. A12603.

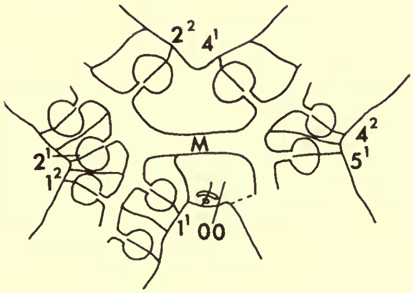


FIG. 25. *Tetracystis oblongus* (Forbes). Sketch of apical region of theca. M, approximate position of mouth ; OO, position of exposed portions of some of the oral plates. Based on specimen SM. A.10140.

The periproct is surrounded by four plates, which are in increasing order of contribution to the border; L4, IL4, IL5, L5. L4 only just reaches the periproct as in some examples of *Staurocystis*. There is no periproct hood in L5. The periproct consists of an anal pyramid of 5 or 6 anals surrounded by a closed circlet of auxiliaries. These are unequally developed so the border of the anal pyramid is narrower adapically as shown in Text fig. 22. There were 9 or 10 auxiliaries in the lectotype and probably more in BMNH. E.29075. Both types of plate may have been slightly ornamented with irregular ridges.

The gonopore and hydropore are apical, presumably developed across the suture between OO1 and 7. Both are inconspicuous and it is impossible to confirm the multiple perforations of the gonopore described by Schuchert (1904).

No complete stem has been seen so it is impossible to confirm that a root structure was developed but this seems likely. SM. A12603 has 10 outer proximals preserved. All have a smooth external flange.

Genus ***PRUNOCYSTITES*** Forbes 1848

Type species. *Prunocystites fletcheri* Forbes 1848.

Diagnosis. A genus of Staurocystinae with (probably 4) short ambulacra confined to apex of theca ; with few relatively long and slender brachioles.

This genus was erected by Forbes to contain the single species *P. fletcheri*, of which at the time only the holotype (SM. A10187) was available. The genus was therefore based on this single specimen which is partly buried in matrix and hence, as Forbes stated (1848 : 503), the original description was imperfect. The holotype, and all subsequently found specimens, are small and it is difficult to assess whether they are immature or adult and, if they are immature, which characters are the result of immaturity. Only one of the specimens available is isolated from the matrix and this has several plates obscured. If all the available specimens are conspecific it is possible to build a composite picture of the characters of the genus, but it must be emphasized that this picture is composite.

Forbes (1848 : 503–504) did not discuss the affinities of *P. fletcheri* but later (1848 : 526) he placed it in a position intermediate between *Echinoencrinites* s.l. and *Pseudocrinites* s.l. which roughly correspond to the Echinoencrinitidae and Staurocystinae. Jaekel (1899) considered *P. fletcheri* and "*Echinoencrinites*" *baccatus* Forbes to be congeneric and therefore assigned the latter to *Prunocystites*, and both species to his family Scoliocystidae (=Echinoencrinitidae). This course has been accepted subsequently. "*E.*" *baccatus* is commoner than *P. fletcheri* and its characters are better known. The concept of *Prunocystites* has therefore been partly based on this species which undoubtedly belongs in the Echinoencrinitidae s.l., where it was placed by Forbes. This accounts for *Prunocystites* having been considered as an echinoencrinitid.

P. fletcheri differs from all other British Callocystitids in having ambulacra confined to the apex of the theca but this could be the result of the small size (? and immaturity) of the thecae known. If the specimen figured in Pl. 9, fig. 10 is really *P. fletcheri* it would indicate that this is a feature of immaturity. The staurocystinid type of ambulacrum can be confirmed in the holotype of *P. fletcheri* if it is wetted with alcohol and examined under a fairly high magnification. On this evidence the genus *Prunocystites* is transferred to the Staurocystinae. There emerges the possibility that all or some of the thecae grouped under *P. fletcheri* are young specimens of other staurocystinid species. They are not young of *Pseudocrinites bifasciatus* which are well known and easily recognized. The long, slender and relatively widely spaced brachioles would seem to preclude *Staurocystis quadrifasciatus* and *Tetracystis oblongus* but young specimens of these species are apparently unknown.

In view of the general uncertainty about *Prunocystites* it is suggested that the name be retained for the specimens described below until such time as it may become possible to settle the characters and affinities of the genus. This leaves "*E.*" *baccatus* Forbes without a genus and, as there is no other name available, the genus *Glansicystis* nov. (*glans* = acorn) is proposed for it (see p. 344).

Prunocystites fletcheri Forbes

(Pl. 3, figs. 8, 9 ; Pl. 8, fig. 4 ; Pl. 9, fig. 11, ?10 ; Text-figs. 26–29)

1848 *Prunocystites fletcheri* Forbes : 504, pl. 16, figs. 1–4.
1854 *Prunocystites fletcheri* Forbes ; Murchison : 217, text-fig. 37, fig. 3.
1857 *Prunocystites fletcheri* Forbes ; Pictet : 299, pl. 99, fig. 16 (2 figs.).
1867 *Prunocystites fletcheri* Forbes ; Murchison : 222, text-fig. 55, fig. 3.
1868 *Prunocystites fletcheri* Forbes ; Bigsby : 26.
1873 *Prunocystites fletcheri* Forbes ; Salter : 127.
1876 *Prunocystites fletscheri* (sic) Forbes ; Quenstedt : 685, pl. 113, fig. 90.
1891 *Prunocystites fletcheri* Forbes ; Woods : 43.
1899 *Prunocystites fletscheri* (sic) Forbes ; Jaekel : 282.
1900 *Prunocystites fletcheri* Forbes ; Bather : 60, text-fig. 24.
1943 *Prunocystites fletcheri* Forbes ; Bassler & Moodey : 53, 185.

DIAGNOSIS. As for the genus.

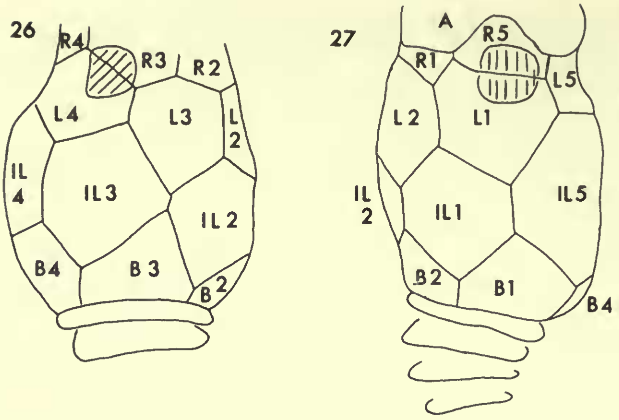
HOLOTYPE. SM. A10187.

MATERIAL. BMNH. 40207, 57395–96 ; DL. 307 ; SM. A.10187–88, A.12579 ; ?BU. IVa.25.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs.

DESCRIPTION. The theca is ovate and very small, being only 5 mm. high in the holotype. The brachioles are developed apically on short ambulacra that protrude from the theca. The mouth was presumably apical, the anus lateral and high up on the theca. The gonopore and hydropore are unknown. In all but one theca there are only two rhombs, B2 : IL2 being undeveloped. The proximal stem is nearly as wide as the theca in some cases, tapers rapidly and is very short. The distal stem in SM. A10188 is very long and slender.

The thecal plates are arranged in a definite order and although it has not been possible to confirm the complete arrangement in any one specimen a composite picture may be built up from the specimens available. This composite picture suggests

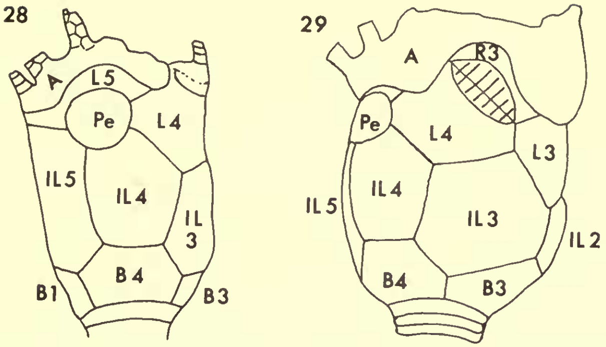


FIGS. 26, 27. *Prunocystites fletcheri* Forbes. Fig. 26. Camera lucida drawing of thecal plates visible in holotype. SM. A.10187. Fig. 27. Camera lucida drawing of thecal plates visible in specimen SM. A.10188. A, ambulacrum; BB, basals; ILL, infralaterals; LL, laterals; RR, radials. Note there is no rhomb B2 : IL2.

that the arrangement was the same as in other species of Staurocystinae but a certain amount of variation occurs. The arrangements of the plates visible in three specimens are shown in Text figs. 26–29. The basals unite abapically to form a cicatrix, the ILL and LL circlets are closed but the exact arrangement of the RR and OO is incompletely known. SM. A12579 and DL. 307 show thecal plates ornamented with fine tubercles and larger tubercles at the umbones of the ILL plates. L5 interrupts the RR. circlet in DL. 307.

Two pectinirhombs are present in all but BU. IVa 25 which is quite probably not a specimen of this species. The shape and degree of separation of the half-rhombs vary considerably and are difficult to interpret. BMNH. 40207 shows half-rhomb L4 well and although it is very small it is completely surrounded by a strong raised rim This suggests that the rhomb is fully developed and by inference that the theca was fully grown, although only 5 mm. high. SM. A12579 shows the same rhomb. It is nearly twice as wide (1·7 mm. as opposed to 1·0 mm.) completely conjunct and somewhat angular. This suggests the rhomb was incompletely developed and therefore that the theca was immature. L1 : R5 is distinctly disjunct in BMNH. 40207 but apparently conjunct in the holotype. No rhomb has been seen with more than 7 dichopores in it. In SM. A12579 the slits were 0·07 mm. wide and separated by 0·125 mm. in half-rhomb R3.

The peristomial area is not clearly visible in any specimen but there were definite ambulacra which protruded from the theca. These are best seen in SM. A12579 and DL. 307 where they are confined to the apical region and each ambulacrum has 4 to 6 brachioles. Three ambulacra can be seen and the flooring plates can be distinguished. The brachioles are long and slender, reaching 12 mm. in DL. 307 and tapering from 0·53 mm. wide at the base to 0·47 mm. at the tips. There are at least 44 brachiolars in the most complete brachioles of DL. 307 and the holotype and



Figs. 28, 29. *Prunocystites fletcheri* Forbes. Fig. 28. Camera lucida drawing of posterior lateral view. Fig. 29. Camera lucida drawing of right lateral view. Note the protruding ambulacra confined to the apex of the theca. A, ambulacrum; BB, basals; ILL, infra-laterals; LL, laterals; Pe, periproct; RR, radials. SM. A.12579.

they are individually rather tall and slender. The cover plates of the brachioles are small and pentagonal. There are approximately three to every brachiolar.

The periproct is close to the ambulacra and high up on the theca. This may be a feature of immaturity. In SM. A12579 and DL. 307 the periproct is surrounded by four plates: IL4, IL5, L4 and L5 but in BMNH. 57396 IL4 does not reach the periproct. In the latter specimen there is an anal pyramid of 6 anals and a complete outer circlet of auxiliaries, probably 10 in number. In SM. A12579 the details are not clear but there appears to be only an anal pyramid.

The gonopore and hydropore have not been detected.

The stem is composed of proximal and distal portions. In SM. A10188, which has the most complete stem known, the proximal portion is composed 12 columnals, 6 outer and 6 inner. It is 1·6 mm. long and tapers from 1·25 mm. to 0·6 mm. in this distance. The distal portion is composed of an unknown number of tall thin columnals, tapers from 0·6 mm. to 0·5 mm. and the preserved portion is 28 mm. long. The holotype has 16 proximals, the outer proximals being provided with a smooth external flange aborally. BMNH. 57395, the largest theca that can definitely be assigned to this species, has 20 proximals.

Subfamily **APIOCYSTITINAE** Jaekel 1899

Diagnosis. A subfamily of Callocystitidae with 4 or 5 ambulacra developed in shallow grooves in thecal plates, not strongly protruding.

Genus ***APIOCYSTITES*** Forbes 1848

Type species. *Apiocystites pentrematoides* Forbes 1848.

Diagnosis. A genus of Apiocystitinae with open circlet of radials; 3 or 4 plates surrounding periproct; four ambulacra all reaching the column; three small pectinirhombs.

Both Regnéll (1945 : 92) and Kesling (1963 : 111) state the following :

1. LL and RR circlets closed.
2. Periproct surrounded by three plates (not L4 according to Kesling).
3. Regnéll adds that ILL4 and 5 are not elongated.

Forbes (1848) described this genus and attributed to it the single species *A. pentrematoides* which becomes type species by monotypy. In this species the RR circlet is open, L5 being inserted between R4 and R5, the periproct is surrounded by four plates, namely ILL4 and 5, and LL4 and 5, and finally ILL4 and 5 are elongated in an ad-abapical direction.

The genus *Apiocystites* has been considered to be synonymous with *Lepocrinites* Conrad, 1840 (=*Lepadocrinus* of authors). This latter genus is said to have LL and RR circlets closed and the periproct surrounded by three plates (not L4). It also differs from *Apiocystites* in having ambulacra which do not reach the stem, and in having larger, angular pectinirhombs. In Regnéll's scheme for the Apiocystitinae (1945 : 91) there are only two genera which have an open RR circlet and four plates around the periproct. These are *Tetracystis* Schuchert 1904 and *Jaekelocystis* Schuchert 1903. It is also necessary to compare the present genus with *Lovenicystis* Regnéll 1945, the type species of which has been described as a species of *Apiocystites*.

Tetracystis differs in having protruding ambulacra which are developed on smooth bands on the theca and are characteristic of the Staurocystinae. It also has large angular pectinirhombs with a relatively large number of dichopores. *Jaekelocystis* differs in having specialized pectinirhombs in which one half is reduced to a small pore 0·5 mm. in diameter. *Lovenicystis* differs in having irregular ambulacra which do not reach the stem in all cases, (which do and which do not varies with the individual), in having larger angular rhombs and an incomplete circlet of auxiliaries in the periproct. This latter feature is found rarely in *A. pentrematoides*.

Apparently despite the changes in the diagnosis of the genus *Apiocystites* that have become necessary after re-examination of the type species, it has no junior synonyms and remains a distinct genus. Bassler & Moodey (1943) accepted four species of *Apiocystites* including the type species of *Lovenicystis*. Of the remaining three species it has not been possible to trace a description of *A. anna* Safford and consequently it is impossible to comment on it. *A. elegans* Hall 1851, judging from the figures, is closely related but apparently differs in having three plates around the periproct. This is not a very reliable character (it varies in *Staurocystis quadrifasciatus*) and so the diagnosis has been extended to include this species.

Apiocystites pentrematoides Forbes

(Pl. 5, figs. 8–10 ; Pl. 6, figs. 1–10 ; Pl. 7, fig. 1 ; Pl. 10, figs. 9, 14 ; Text-figs, 30–35)

1848 *Apiocystites pentrematoides* Forbes : 503, pl. 15, figs. 1–9.
1854 *Apiocystites pentrematoides* Forbes ; Murchison : 217, text-fig. 37, fig. 4.
1857 *Apiocystites pentrematoides* Forbes ; Pictet : 298, pl. 99, fig. 14*a–c*.
1867 *Apiocystites pentrematoides* Forbes ; Murchison : 222, text-fig. 55, fig. 4.
1868 *Apiocystites pentrematoides* Forbes ; Bigsby : 24.
1873 *Apiocystites pentrematoides* Forbes ; Salter : 127 (1 fig.).

1876 *Apiocystites pentrematoides* Forbes ; Quenstedt : 680, pl. 113, fig. 80.
1891 *Apiocystis pentremitoides* (sic) (Forbes) Carpenter : 9, 10 (5 figs.), 81.
1899 *Apiocystites pentrematoides* Forbes ; Jaekel : 282, pl. 15, fig. 2.
1904 *Apiocystites pentrematoides* Forbes ; Schuchert : 211.
1943 *Apiocystites pentrematoides* Forbes ; Bassler & Moodey : 52, 130.

DIAGNOSIS. An *Apiocystites* with four plates surrounding periproct.

HOLOTYPE. BMNH. 40187.

MATERIAL. More than 45 specimens in BMNH., BU., GSM., OUM., ?RSM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs.

DESCRIPTION. The theca is ovate elongate and somewhat rounded in cross-section. The mouth, hydropore and gonopore are apical and the anus lateral. The stem was provided with a root structure. The ambulacra are inconspicuous as they are developed in shallow grooves and are flush with the surface of the thecal plates.

The thecal plates are arranged in the usual manner and the arrangement of the first four circlets is as in Text-fig. 30. The arrangement of the orals and adjacent ambulacral flooring plates is shown in Text-fig. 32. There is some variation in the exact position of the ambulacra but little variation in the thecal plating arrangement.

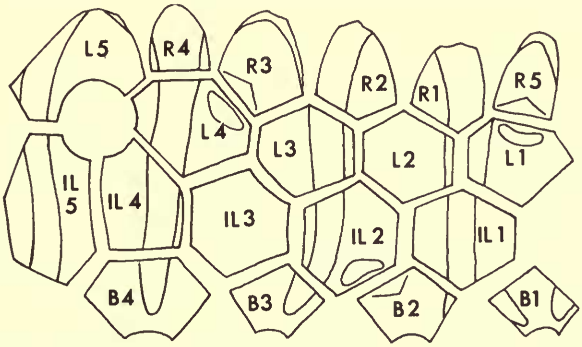


FIG. 30. *Apiocystites pentrematoides* Forbes. Sketch of the arrangement of thecal plates of first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.12601.

The basals combine abapically to form a circular cicatrix about 4 mm. in diameter in SM. A12601. Unlike the majority of species of Callocystitidae described the thecal plates are ornamented with fine tubercles and not irregular ridges. This ornamentation is not developed in the shallow curved grooves in which the ambulacra lie. These grooves are smooth and show faint traces of the outlines of the overlying ambulacral flooring plates.

The usual three disjunct pectinirhombs are present. When immature these rhombs tend to be subangular in outline but more often the half-rhombs are distinctly rounded.

B2 : IL2 SM. A12599. This is a compressed rhomb, with distinctly separated halves and measures 3·0 mm. by 2·35 mm. externally. It has 9 dichopores in a

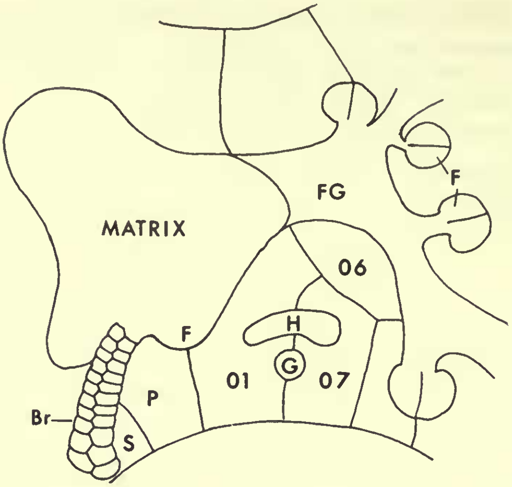


Fig. 31. *Apiocystites pentrematoides* Forbes. Camera lucida drawing of apical region, showing arrangement of food grooves, facets and visible portions of oral plates. Br, brachiole ; F, facet ; FG, food groove ; G, gonopore ; H, hydropore ; OO, orals ; P, primary flooring plate ; S, secondary flooring plate. SM. A.12601.

width of 1·93 mm., the longest reaching 2·47 mm. The slits in B2 are 0·095 mm. wide, separated by 0·10 mm. and reach a length of 0·75 mm. Those in IL2 are obscured by matrix but could not have exceeded 0·5 mm. in length.

L1 : R5 SM. A12601. This is a slightly immature, angular, rhomb and it is depressed. It measures 2·0 mm. by 2·2 mm. externally and has 9 dichopores in a width of 1·9 mm., the longest reaching 1·47 mm. The slits in L1 are 0·14 mm. wide and separated by 0·07 mm. while those in R5 are 0·09 mm. wide and separated by 0·125 mm. The slits in L1 reach a length of 0·47 mm. while those in R5 reach 0·6 mm.

L4 : R3 SM. A12601. This is an equal symmetrical rhomb measuring 2·2 mm. by 2·2 mm. It has 9 dichopores in a width of 1·8 mm., the longest reaching 2·63 mm. The slits in L4 are slightly wider than those in R3 and also shorter.

The mouth was elongate, slightly curved and placed apically at the union of the ambulacra. It was surrounded by the usual 7 orals plates arranged as in Text-fig. 32. The ambulacra are relatively narrow and, in SM. A12601, taper gradually from 1·6 mm. wide apically to about 1·0 mm. at their tips. They broaden considerably apically forming an area 4·2 mm. by 3·3 mm. around the mouth in this specimen. They are developed in shallow grooves and constructed in the same way as other callocystitid ambulacra. They differ from the other species described in having the secondary flooring plates about half the size of the primaries and regularly reaching the ambulacral mid-suture (see Text-fig. 34). The main food groove is relatively narrow and gives off lateral food grooves at a very oblique angle. This adds to the different appearance of this type of ambulacrum (see Text-fig. 33). The flooring plates are apparently unornamented between the lateral food grooves. Both types

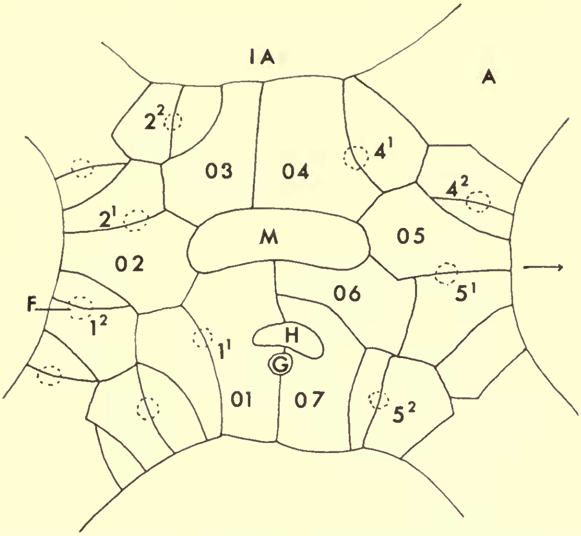
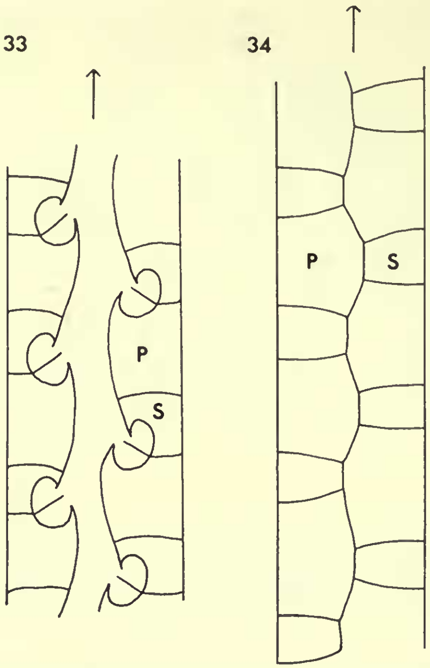


FIG. 32. *Apiocystites pentrematoides* Forbes. Camera lucida drawing of apical region of a weathered specimen, showing arrangement of oral plates and adjacent ambulacral flooring plates. A, ambulacrum ; F, position of facets ; G, gonopore ; H, hydropore ; IA, inter-ambulacrum ; M, mouth ; OO, orals. The arrow points to the periproct. BU., unregistered.

of food groove are provided with small cover plates which are also unornamented. The brachiole facets are small circular pits in the flooring plates. The brachioles are slender and relatively widely spaced. This last feature varies considerably. The average of ten measurements was 4 brachioles in 4·72 mm. but varied from 4 in 3·73 mm. to 4 in 5·6 mm. The brachioles may reach 2·7 mm. in length and are only 0·3 mm. wide at the base. They are composed of approximately 30 brachiolars.

The periproct is surrounded by four plates which are : ILL4 and 5 and LL4 and 5. L5 contributes approximately a third of the border, and the other three contributing about equally to the remaining two-thirds. There is no periproct hood in L5. The periproct is almost level with the general surface of the theca and 1·6 mm. in diameter in SM. A12601. Within the narrow but complete circlet of auxiliaries in this specimen there is a slightly elevated anal pyramid 1·3 mm. in diameter and composed of 6 anals. In some examples the auxiliary circlet may be incomplete. This is the case in BMNH. 57392 where there are only 5 auxiliaries abapically. In the complete circlet of BMNH. 40188 there are only 6 auxiliaries and 7 in BMNH. 25533 and E.29074. Both the anals and auxiliaries are unornamented.

The gonopore and hydropore are apical and shared by O1 and O7. The hydropore is semicircular and somewhat slit-like and is adapical to the gonopore. In BMNH. 40153 the gonopore is covered by a pyramid of 4 gonals (see Text-fig. 35). The hydropore and gonopore may be quite separate as in SM. A12601 (Text-fig. 31) or the hydropore may be wrapped around the gonopore as in BMNH. 40153 (Text-fig. 35).



Figs. 33, 34. *Apiocystites pentrematoides* Forbes. Fig. 33. Sketch of part of an ambulacrum. Based on specimen SM. A.12599. Fig. 34. Sketch of impression of ambulacral flooring plates on the thecal plates. P, primary flooring plate ; S, secondary flooring plate. The arrows point to the mouth. Based on specimen SM. A.12597.

The stem is typical of the Callocystitidae but from what is known the distal portion is reduced, and may merge gradually into the proximal portion. SM. A12599 has a complete stem terminating in a root structure (see Pl. 10, fig. 14). It is 20 mm. long compared with a thecal height of 15 mm. The proximal portion is relatively large,

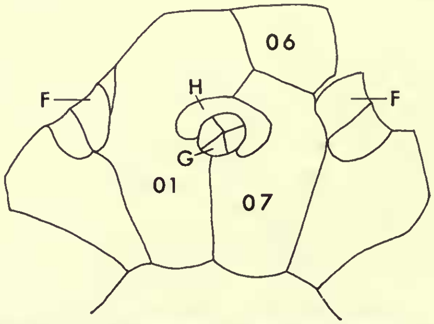


Fig. 35. *Apiocystites pentrematoides* Forbes. Sketch of the area around the gonopore and hydropore, showing gonopore closed by pyramid of four gonals and closely approximated to hydropore. F, facet ; G, gonopore ; H, hydropore ; OO, orals. Cf. Text-fig. 31. Based on specimen BMNH. 40153.

at least 13 mm. long, and tapers from 4·5 mm. at the base of the theca to about 2·5 mm. The distal portion is very short and narrow. In BMNH. 48192 the stem is shorter than the thecal height and the distal portion consists of only 5 columnals. There are 8 outer proximals in this specimen and 17 or 18 in SM. A12601. The outer columnals are provided with an external flange which is slightly beaded with fine tubercles in well preserved examples.

Family **ECHINOENCRINITIDAE** Bather 1899

Diagnosis. A family of Glyptocystitida with typically produced periproct composed of anal pyramid and single circlet of auxiliaries ; with short ambulacra restricted to apex of theca. Modified from Kesling (1963).

Within this family the rhombs are all disjunct pectinirhombs, but there are two different types. In *Echinoencrinites*, and the other Ordovician genera except *Scoliocystis*, all the dichopores of each rhomb are discrete entities and they open externally in slits which are level with the surface of the thecal plates. The slits are isolated from each other and provided individually with very narrow raised rims. In the Silurian genera, and *Scoliocystis*, the walls of individual dichopores in a rhomb are continuous with those of the adjacent dichopores at the external surface and the dichopores are effectively folds in the thecal plates. All the slits of one half-rhomb open in a depression or *vestibule* which is provided, as a whole, with a raised rim. This rim is open in one half-rhomb and closed in the other. The *Echinoencrinites* type of disjunct pectinirhomb was common in the Ordovician but the other type predominates in the Silurian and Devonian. The latter type was more efficient and was independently acquired by several families of Glyptocystitida. If Jaekel's figures of *Scoliocystis* (Jaekel 1899, pl. 11, figs. 10, 10*a*, 11) are accurate then it must be the ancestor of the British Silurian echinoencrinitids, and these three genera may be distinguished from the others by their advanced type of pectinirhomb. Jaekel (1899) proposed the family Scoliocystidae which was unfortunately pre-occupied by Bather's Echinoencrinitidae published earlier in the same year. The name is now resurrected for a subfamily of the Echinoencrinitidae containing the genus *Scoliocystis*. The Echinoencrinitidae may therefore be divided into the following two subfamilies :

Subfamily **ECHINOENCRINITINAE** nov.

Diagnosis. A subfamily of Echinoencrinitidae with disjunct pectinirhombs composed of dichopores opening as discrete slits, individually surrounded by slight rims and level with external surface of thecal plates.

Subfamily **SCOLIOCYSTINAE** Jaekel 1899 emend

Diagnosis. A subfamily of Echinoencrinitidae with disjunct pectinirhombs composed of dichopores opening as slits within vestibules, collectively surrounded by a rim.

Genus ***GLANSICYSTIS*** nov.

As stated earlier the removal of *Prunocystites fletcheri* from the Echinoencrinitidae to the Staurocystinae necessitates the description of a new genus for "*Echinoencrinites*" *baccatus* Forbes.

DIAGNOSIS. A genus of Scoliocystinae with ovate theca, four plates surrounding periproct, L5 interrupting the RR circlet, three pectinirhombs.

TYPE SPECIES. *Echinoencrinites baccatus* Forbes 1848.

Glansicystis baccata (Forbes)

(Pl. 7, figs. 2–18 ; Pl. 8, figs. 1–3 ; Pl. 10, figs. 10, 11 ; Text-figs. 36–39)

1848 *Echinoencrinites baccatus* Forbes : 506, pl. 17, figs. 1–11.
1854 *Echinoencrinites baccatus* Forbes ; Murchison : 217, text-fig. 37, fig. 5.
1857 *Echinoencrinites baccatus* Forbes ; Pictet : 300.
1867 *Echinoencrinites baccatus* Forbes ; Murchison : 222, text-fig. 55, fig. 5.
1868 *Echinoencrinites baccatus* Forbes ; Bigsby : 25.
1873 *Echinoencrinites baccatus* Forbes ; Salter : 128.
1876 *Echinoencrinus baccatus* (Forbes) Quenstedt : 676, pl. 113, fig. 70. (3 figs.).
1896*a* *Echinocystis baccata* (Forbes) Haeckel : 146.
1899 *Prunocystites baccatus* (Forbes) Jaekel : 263.
1900 *Prunocystites baccatus* (Forbes) ; Bather : 60.
1943 *Prunocystites baccatus* (Forbes) ; Bassler & Moodey : 53, 184.

DIAGNOSIS. As for the genus.

LECTOTYPE. GSM. 7380. The original specimen of Forbes (1848, pl. 17, figs. 1, 3, 4).

MATERIAL. About 30 specimens of which three (BMNH. E.29057 ; GSM. 7380, 103101) are of the typical form. These are in BMNH., BU., GSM., OUM., SM.

HORIZON AND LOCALITY. Wenlock Limestone, Middle Silurian ; Dudley, Worcs. and Walsall, Staffs.

DESCRIPTION. The theca is elongate ovate with brachioles developed apically around the mouth. The anus is lateral and just over half way up the theca while the

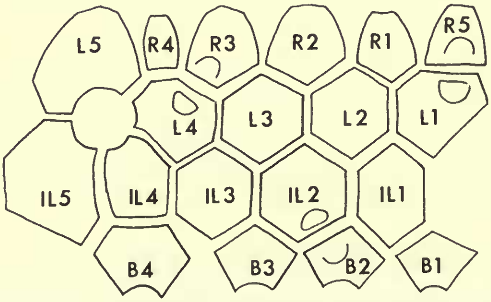


FIG. 36. *Glansicystis baccata* (Forbes). Sketch of arrangement of thecal plates of first four circlets. BB, basals ; ILL, infra-laterals ; LL, laterals ; RR, radials. Based on specimen SM. A.12578.

gonopore and hydropore are apical. Three disjunct pectinirhombs and the usual type of stem are present.

The thecal plates are arranged in definite circlets and the usual formula may be given. The typical plating arrangement of the first four circlets is shown in Text-fig. 36. There is considerable variation however. Text-fig. 37 shows an arrangement in which ILL1–4 form a closed circlet and Text-fig. 38 another unusual arrangement in which there are 6 RR and L5 does not interrupt the RR circlet. Both these specimens appear to be anomolous. The four basals combine abapically to form a circular cicatrix 4 mm. in diameter in SM. A12577. There were 7 orals, 6 of which reach the peristome and contribute to its margin, as in the other Glyptocystitida. The odd oral is O7 (Text-fig. 39). The size of the area occupied by the orals varies and is associated with two distinct trends within this species. In the lectotype and two other specimens (GSM. 103101, BMNH. E.29057) the area occupied by the orals is small (Pl. 7, fig. 8) while in the other examples this area is larger (Pl. 7, fig. 2). The plates of the type and the two examples mentioned above are ornamented with ramifying irregular raised pustules while those of all other specimens are ornamented with fine granules. There is also a tendency for the plates of the typical form to be much more tumid and the sutures deeper than in the other form.

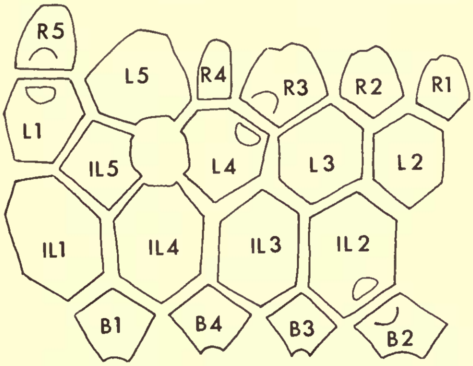


FIG. 37. *Glansicystis baccata* (Forbes). Sketch of unusual arrangement of thecal plates in which IL5 has been elevated in the theca allowing ILL1–4 to form a closed circlet. BB, basals; ILL, infra-laterals; LL, laterals; RR, radials. SM. A.12577.

There are three disjunct pectinirhombs with half-rhombs with semi-circular outlines. All have few dichopores and prominent rims which are closed on IL2, L1 and L4. These rims are more strongly developed on the typical form than on the others.

B2 : IL2 BMNH. E.29057. This is a compressed rhomb measuring 2·8 mm. by 2·3 mm. with 8 dichopores in a width of 1·73 mm., the longest reaching 2·23 mm. The slits in both B2 and IL2 are 0·09 mm. wide and separated by 0·125 mm. In both half-rhombs they reach a maximum length of 0·65 mm.

L1 : R5 (Lectotype). This is a compressed rhomb measuring 3·53 mm. by 2·8 mm. externally with 8 dichopores in a width of 1·73 mm. The extra millimetre in the width is entirely taken up by the prominent rhomb rim in L1. The longest dichopore is approximately 1·75 mm. long. The slits in L1 are 0·107 mm. wide and separated by 0·125 mm. while those in R5 are only 0·07 mm. wide and separated by 0·14 mm. The slits in L1 reach a maximum length of 0·6 mm. and those of R5 marginally longer. The same rhomb in SM. A12577 is highly compressed, being twice as long as wide, has 7 dichopores and a much less conspicuous rim on L1.

L4 : R3 (BMNH. E.29057). This is a compressed rhomb measuring 4·33 mm. by 3·05 mm. with 10 dichopores in a width of 2·47 mm., the longest reaching 3·0 mm. The slits on L4 are obscured by matrix but those on R3 are 0·07 mm. wide and separated by 0·14 mm. They reach a length of approximately 0·75 mm. The same rhomb in SM. A12577 has only 8 dichopores, a much less conspicuous rim on L4, and is again more distinctly compressed.

The ambulacra in the typical form are restricted to the oral plates and give rise to two large, and possibly two small, facets in the lectotype. In the other form the ambulacra may extend on to radial plates (Pl. 7, fig. 2) and have up to 3 facets in one ambulacrum. The maximum number of facets seen was 7. There may well be four ambulacra of which 1 and 4 terminate in a single large facet (the first formed) while ambulacra 2 and 5 may add up to three facets. This interpretation is not certain. The orals are ornamented between the ambulacra in the same way as the other thecal plates. The food grooves are broad and deep and covered by alternating cover plates which are unornamented. Apparently the cover plates were unable to articulate with the orals or flooring plates and were lodged in grooves in these plates. These grooves enlarged as the ambulacra grew. The mouth is a more or less central, oval opening. The facets are set in quite deep depressions in the oral or flooring plates. The brachioles are preserved in BU. H063 where they are at least 12 mm. long (none appears to be complete) and are composed of at least 50 brachiolars. As far as can be determined they do not taper in the preserved portion and are 0·75 mm. wide. The food groove was provided with cover plates and these are 2 to 3 times as numerous as the brachiolars.

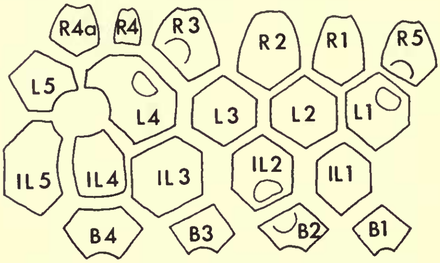


FIG. 38. *Glansicystis baccata* (Forbes). Sketch of unusual arrangement of thecal plates in which there are six radial plates forming a closed circlet. BB, basals ; ILL, infralaterals ; LL, laterals ; RR, radials. BMNH. E.29057.

The periproct is surrounded by four plates which are : ILL4 and 5 and LL4 and 5. Apart from the two anomolous specimens figured in Text-figs. 37 and 38 the arrangement is constant. L5 contributes just less than a third of the border and the other three plates share more or less equally in the remaining two-thirds. In the typical form there appear to be 12 auxiliaries forming a complete circlet but only half this number are found in SM. A12577 and possibly 7 in SM. A12578, still forming a complete circlet. The anal pyramid is composed of 6 anals in SM. A12577, the only specimen in which the number can be made out. The ornament of the auxiliaries, and probably the anals as well, is the same as that of the thecal plates and consequently this is more marked in the typical form.

The gonopore and hydropore are set apically across the common suture of OO1 and 7. The hydropore is elongate, slightly curved and adoral. The gonopore is circular and covered by a gonal pyramid of an unknown number of gonals. In both forms of the species both apertures are set in a diamond shaped depression in OO1 and 7.

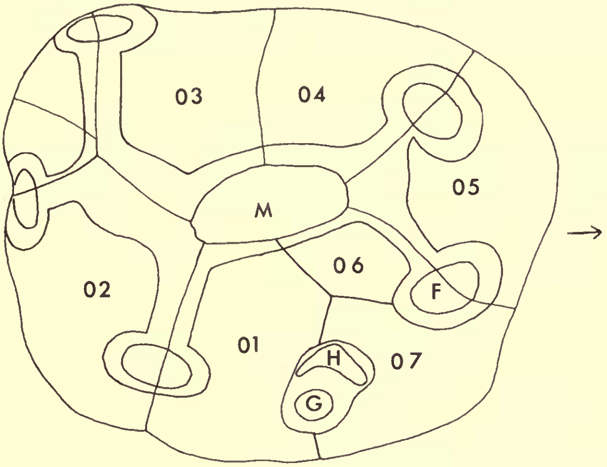


FIG. 39. *Glansicystis baccata* (Forbes). Camera lucida drawing of apical region. F, facet; G, gonopore; H, hydropore; M, mouth; OO, orals. The arrow points to the periproct. Based on specimen OUM. C.518.

The stem is composed of a proximal and a distal portion as in all other Glyptocystitida. A complete stem is preserved in BU. H025. The stem is 12–13 mm. long compared with a thecal height of 10 mm. The proximal portion has 12 outer columnals tapering from just under 3 mm. to half that, in a distance of about 6 mm. The outer proximals are provided with an external flange that may have one or two rings of fine tubercles developed on it. The distal portion is composed of 18 distinct columnals and a few more fused into the root structure. The proximal 8 are in distinct pairs, thereafter the columnals are exceptionally thin. The stem is attached to a polyzoan.

REMARKS. There are two distinct forms of this species, the typical form of the lectotype, and the common form. The possibility that these represent two distinct species cannot be ruled out. Unfortunately there are only three specimens of the typical form which is too small a number to give an accurate impression of the variation. Even so, one of these specimens has an aberrant plating arrangement (BMNH.

E.29057). The main points of difference are the thecal ornamentation, the area of the orals, the degree of impression of the sutures and consequently the tumidity of the plates, and the strength of the development of the rhomb rims. Thecal ornamentation is very variable in the next species, *Schizocystis armata*, where two analogous variations occur and it does not correlate with any other features. This character would seem to be an unreliable one taxonomically. Some specimens of the common form have tumid plates and relatively deep sutures like the typical form. This leaves only the size of the oral area and the strongly developed rhomb rims. Again in the next species the rhomb rims show considerable variation which is not correlated with any other feature so this too may be unreliable. In view of the wide variation shown by the common form it is thought wise to regard the typical form as merely another variation, albeit more distinct, especially as there are so few specimens on which to base an impression of its variability.

Genus ***SCHIZOCYSTIS*** Jaekel 1895

DIAGNOSIS. A genus of Scoliocystinae with theca ovate aborally and laterally compressed adorally; brachioles on two short ambulacra running anteriorly and posteriorly across top of theca; strongly protruding periproct surrounded by four plates.

TYPE SPECIES. *Echinoencrinites armatus* Forbes 1848.

Schizocystis armata (Forbes)

(Pl. 8, figs. 5–11; Pl. 9, figs. 1–9; Pl. 10, figs. 15, 16; Text-figs. 40–44)

1848 *Echinoencrinites armatus* Forbes : 507, pl. 18, figs. 1–14, pl. 19, figs. 1–10.
1854 *Echinoencrinites armatus* Forbes ; Murchison : 217, text-fig. 37, fig. 6 (3 figs.).
1857 *Echinoencrinites armatus* Forbes ; Pictet : 300, pl. 99, fig. 17 (3 figs.).
1865 *Echinoencrinus armatus* (Forbes) Rofe : 251, pl. 8, figs. 10, 11.
1867 *Echinoencrinites armatus* Forbes ; Murchison : 222, text-fig. 55, fig. 6 (3 figs.).
1868 *Echinoencrinites arenatus* (sic) Forbes ; Bigsby : 25.
1873 *Echinoencrinites armatus* Forbes ; Salter : 127 (fig.), 128.
1875 *Echinoencrinus armatus* (Forbes) ; Bailey : 54, pl. 18, fig. 7.
1876 *Echinoencrinus armatus* (Forbes) ; Quenstedt : 675, pl. 113, figs. 68 (5 figs.), 69.
1891 *Echinoencrinus armatus* (Forbes) ; Woods : 43.
1891 *Echinoencrinus armatus* (Forbes) ; Carpenter : 7, pl. 1, fig. 3.
1895 *Schizocystis armatus* (Forbes) Jaekel : 113.
1896*a* *Echinocystis armata* (Forbes) Haeckel : 140, pl. 4, figs. 31–34.
1899 *Schizocystis armata* (Forbes) ; Jaekel : 266, pl. 12, figs. 1, 1*a–c*, 2.
1900 *Schizocystis armata* (Forbes) ; Bather : 61, text-figs. 25–27.
1943 *Schizocystis armata* (Forbes) ; Bassler & Moodey : 53, 188.
1945 *Schizocystis armata* (Forbes) ; Delpey : 261, text-fig. 8.
1953 *Schizocystis armata* (Forbes) ; Cuénot : 261, text-fig. 19.

DIAGNOSIS. As for the genus.

LECTOTYPE. GSM. 7381 is the original of Forbes (1848, pl. 18, figs. 1–4), and although it is incomplete it is the most suitable specimen here selected as lectotype.

Material About 125 specimens in BMNH., BU., GSM., OUM., RSM., SM. Of these 45 have 2 rhombs, 15 have 3 and 30 are indeterminate. Information is not available for the remainder.

Horizon and locality. Wenlock Shale, Middle Silurian; Dudley, Walsall, Hurst Hill, Malvern, May Hill, Pen-y-lan.

Description. The theca is sac-like, laterally compressed adorally and tumid aborally. The left side is concave or flat adorally and convex aborally, while the right side is gently convex throughout. The mouth was at the confluence of the two short ambulacra which run anteriorly and posteriorly along the crest of the theca. The posterior is the shorter. The gonopore and hydropore are apical on the left side of the theca and the anus is lateral, about half way up the theca. The anus, half-rhomb rims and the umbones of the ILL plates all protrude strongly giving the theca a tubercular appearance. The stem was aboral and lacked a root structure.

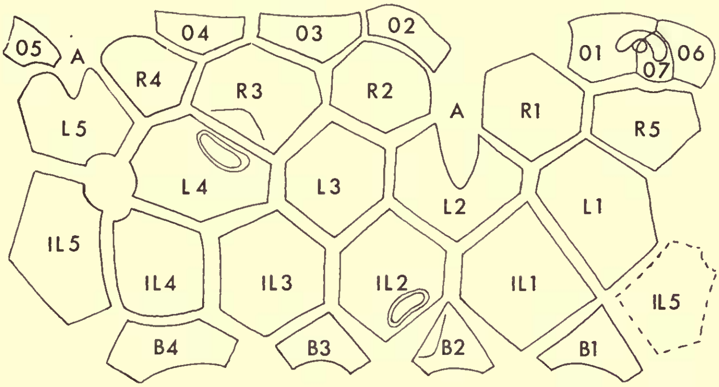


Fig. 40. *Schizocystis armata* (Forbes). AA, ambulacra; BB, basals; ILL, infra-laterals; LL, laterals; OO, orals; RR, radials. Based on specimen SM. A.12592.

The arrangement of the thecal plates is shown in Text-fig. 40, but there is a certain amount of variation in the details. In the specimen illustrated in Text-fig. 40 the ILL only just form a closed circlet, IL1 and IL5 meeting at a point. In several other thecae all the ILL have long common sutures. In SM A10197 (Text-fig. 41) L4 and L3 only just meet at a point and L1 is an unusual shape. Presumably all these variations were related to variability in the total shape and size of the thecae in this species. The lengths of the ambulacra also vary considerably. In SM. A10197 both just reach the lateral plates forming slight embayments in the margins of L2 and L5. In other specimens the ambulacra extend well on to these plates and the posterior may reach the edge of the periproct. This feature is not related to size apparently. The basals have very short common sutures and the pentagonal ones are very sharply pointed. They unite abapically forming a circular cicatrix 5·5 mm. in diameter in SM. A10197. The orals are strung out along the sides of the ambulacra in an unusual arrangement. OO2, 3 and 4 are on the right side of the theca (Text-fig. 42) and OO5, 6, 7 and 1 on the left (Text-fig. 43). The remainder of the ambulacra are composed of flooring plates.

The ornamentation of the thecal plates is very variable (see Pl. 8, figs. 5, 6 ; Pl. 9, figs. 3, 5). In SM. A12592 it is of irregular tubercles and rounded ridges, giving the thecal surface an uneven appearance, and the umbones of the ILL plates are not very strongly developed. In the lectotype the plates are finely granulated and the umbones of the ILL plates are very prominent. This ornament is very common and typical. The strength and density of the granulations varies from plates which appear almost smooth to plates that appear to be prickly. In extreme cases some of the tubercles unite to form strong intermittent radiating ridges as in the specimen figured on Pl. 9, fig. 3.

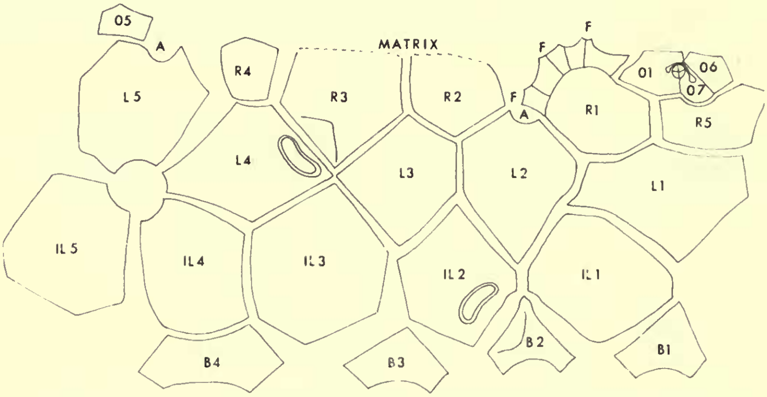


FIG. 41. *Schizocystis armata* (Forbes). Sketch of arrangement of thecal plates. AA, ambulacra ; BB, basals ; F, facet ; ILL, infra-laterals ; LL, laterals ; OO, orals ; RR, radials. SM. A.10197.

There may be two or three rhombs present and the two and three-rhombed forms differ in the details of the gonopore and hydropore, and the adoral portions of the two ambulacra. B2 : IL2 and L4 : R3 are always present but L1 : R5 may or may not be developed. Apparently the three-rhombed form is commoner at Malvern than at Dudley or Walsall but apart from this there is little difference in distribution. At all three localities the two-rhombed form is commoner than the three-rhombed.

B2 : IL2 (SM. A12592). This rhomb is compressed and measures 4·35 mm. by 4·0 mm. externally. It has 15 dichopores. The slits in B2 reach a length of 1·1 mm. They are 0·07 mm. wide and separated by 0·125 mm. The slits of IL2 are obscured by matrix but could not have reached the same length as those in B2.

L4 : R3 (SM. A12592). This rhomb is also compressed and measures 4·5 mm. by 4·0 mm. It has 15 dichopores whose slits reach a length of 1·16 mm. in R3 but only 0·7 mm. in L4. The slits in L4 are slightly wider than those in R3.

SM. A12583 has all three rhombs. B2 : IL2 has 17 dichopores ; L4 : R3 has 12, and L1 : R5 has 10.

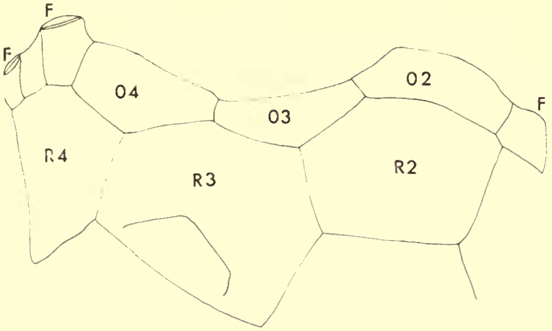


FIG. 42. *Schizocystis armata* (Forbes). Camera lucida drawing of adapical region of right side. F, facet; OO, orals; RR, radials. SM. A.12592.

The mouth has not been directly observed but lay apically at the confluence of the two ambulacra. The anterior ambulacrum was the longer and has three facets to the left in SM. A10197; the posterior having only 2. In SM. A12592 the anterior had 5 smaller facets, 4 to the left and 1 to the right, while the posterior had three facets all to the left of the ambulacrum. Both ambulacra are longer in the latter example although it has a smaller theca. Although there is considerable variation in the length and number of facets the majority of the facets is always to the left of the ambulacrum. Thus the food grooves of the brachioles of the posterior ambulacrum may be inferred to have faced the left of the theca and those in the anterior, the right of the theca.

Near the mouth the oral plates contribute to the ambulacra and these give way distally to the ambulacral flooring plates. There are no facets developed on the oral plates and each facet is formed of two ambulacral flooring plates as in all other Glyptocystitida. In the two-rhombed forms the adoral portion of the food groove forms a gentle curve, concave to the left side of the theca. OO6, 7 and 1 are bent over to fill this concavity and consequently they face directly upwards (see Pl. 9, fig. 1). The gonopore and hydropore also face in this direction. In the three-rhombed forms the adoral portion of the food groove forms an S-shaped curve with the portion above the gonopore and hydropore convex to the left of the theca. OO6, 7 and 1 face to the left of the theca in this form and so do the gonopore and hydropore (see Pl. 9, fig. 7). The food groove was covered with flooring plates which were ornamented with fine pustules. They are relatively large plates and alternate regularly. The lateral food grooves are short and very oblique. Brachioles are preserved on OUM. C.398 and are long and slender. They taper evenly right up to the tip and were composed of about 100 brachiolars. There is no evidence of twisting of the food groove and the brachioles may reach twice the length of the theca.

The periproct was surrounded by four plates which are ILL4 and 5, and LL4 and 5. There is a strongly protruding anal pyramid composed of five anals and surrounded by a complete set of 10 auxiliaries in SM. A10197. The auxiliaries are frequently more strongly developed adorally and to the right than at other points around the periproct and this causes the anal pyramid to point to the left and aborally. This is not univer-

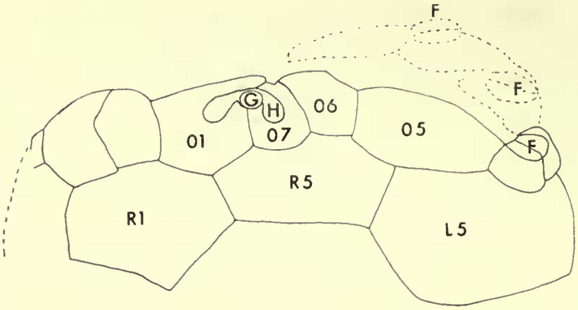


FIG. 43. *Schizocystis armata* (Forbes). Camera lucida drawing of adapical portion of left side. F, facet ; G, gonopore ; H, hydropore ; OO, orals ; RR, radials. SM. A.12592.

sal however. In SM. A10197 the periproct is 2 mm. in diameter and, although incomplete, protrudes 1·2 mm. from the level of the theca.

The gonopore and hydropore lay apically across the common suture of OO1 and 7. The hydropore was curved, bilobed and the adoral of the pair. It was provided with a rim. The gonopore is small, circular and covered with a pyramid of 3 or 4 gonals. In SM. A10197 it is 0·5 mm. in diameter. As previously stated the direction in which these orifices face depends on whether there are two or three rhombs developed.

The stem was typical of the Glyptocystitida being divisible into proximal and distal portions. On SM. A12585 the outer proximals are smooth and ring-like but have an aboral ring of fine tubercles. One GSM. specimen has slightly compressed proximals with a slight crest developed posteriorly but this could be aberrant. In OUM. C398 the distal columnals are smooth and differ from the proximals in being taller and thinner. The stem gradually tapers throughout its length. BMNH. 57442 has a virtually complete stem. It is about 32 mm. long and tapers from 4 mm. at the base of the theca to approximately 0·5 mm. at the tip. The proximal portion has 11 outer proximals provided with a ring of fine tubercles aborally. There are 26 to 28 distals which alternate regularly, the larger being provided with a central ring of tubercles developed on a distinct flange. The distal portion tapers regularly to a point.

SM. A8137*a* is an internal mould of a specimen from the May Hill inlier. It is preserved in a light brown material and clearly shows the plate margins etc. Developed somewhat irregularly over the surface is a reticular pattern of dark brown lines. These lines are composed of a different material to the rest of the internal mould and appear to be just too regular to be preservational in origin yet not quite regular enough to be certain they are organic in origin. The pattern is indicated in Text-fig. 44 and the lines appear to form a ring in the centres of the plates and to give off one, or rarely two, trans-sutural branches which join up with the central ring of the neighbouring plates. The significance of this pattern is not understood. The associated specimen from the same piece of rock does not show this feature on its internal mould (Pl. 9, fig. 8).

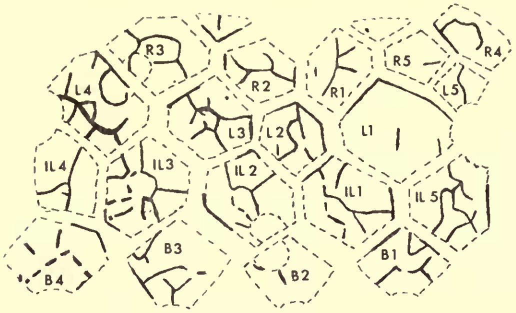


FIG. 44. *Schizocystis armata* (Forbes). Sketch of thecal plates of internal mould, showing reticular structure described in text. The specimen is unusual in having 5 plates surrounding the periproct, but as it is an internal mould direct comparisons with external views cannot be made. SM. A.8137*a*.

REMARKS. As with the preceding species there are two fairly distinct forms of this species, which may be referred to as the two- and three-rhombed forms. These two forms are thought to have had slightly different modes of life but this cannot of course be confirmed. There is considerable difficulty in envisaging a mode of life which explains satisfactorily all the morphological adaptations of this species let alone imagining two for a pair of ecological subspecies which these two forms may well represent. As with the last species it is thought wiser to refer all the specimens to a single species while recognizing that two more or less distinct forms occur. It is not thought that these two forms could represent sexual dimorphism in *Schizocystis* as there is no significant difference in the gonopore of the two forms, which might be expected in that case.

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